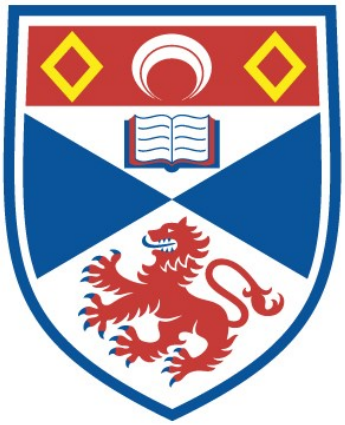
LIGHT, TEMPERATURE AND THE INDUCTION OF DORMANCY IN 'POTAMOGETON CRISPUS' AND 'POTAMOGETON OBTUSIFOLIUS'

Patricia A. Chambers

A Thesis Submitted for the Degree of PhD
at the
University of St Andrews



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LIGHT, TEMPERATURE AND THE INDUCTION OF DORMANCY IN *POTAMOGETON CRISPUS* AND *POTAMOGETON OBTUSIFOLIUS*

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ABSTRACT

Dormancy in many aquatic angiosperms is characterized by the production of turions, specialized vegetative buds which function as both propagules and perennating organs. In temperate climate species, induction of dormancy is usually associated with short days, often in conjunction with low temperatures. By contrast, the turions of Potamogeton crispus are formed around midsummer and the species grows luxuriantly throughout the winter.

The environmental factors controlling turion formation in Potamogeton crispus were investigated under natural and laboratory conditions. Potamogeton obtusifolius, a typical temperate climate species exhibiting autumnal turion production, was studied for comparative purposes. Phenological development of natural populations in two Scottish lakes was compared with seasonal measurements of temperature, daylength, underwater light attenuation and light quality (the red and far red wavelength bands). Temperature and photoperiod were identified as the primary environmental factors regulating turion formation in both species. Laboratory experiments confirmed the field observation that turions are produced by Potamogeton crispus in response to long days (greater than 12 to 16h) and high temperatures (greater than 16^{o}C). In Potamogeton obtusifolius, turion production is associated with short days and high temperatures.

Because of the complexity of the underwater light climate, the effect of light quantity (irradiance) and light quality on turion production could not be determined. Laboratory experiments showed that under inductive photoperiodic and temperature conditions, low red:far red ratios and low irradiance inhibited turion formation in

Potamogeton crispus. The action of phytochrome in the perception of the long day photoperiodic signal and the quantitative effect of sucrose concentration on the magnitude of turion production in Potamogeton crispus was investigated.

A model of phytochrome action in the control of photoperiodic and photomorphogenetic responses in aquatic angiosperms is presented and the role of turions in the life history of Potamogeton crispus and Potamogeton obtusifolius is assessed.

SUPERVISOR'S CERTIFICATE

I certify that Patricia A. Chambers has spent 12 terms of research under my supervision, that she has fulfilled the conditions of Ordinance General No. 12 and Resolution of the University Court 1967 No. 1, and that she is qualified to submit this thesis for the degree Doctor of Philosophy.

D.H.N. Spence

St. Andrews, February 1982

DECLARATION

I declare that this thesis is a record of my own work and that it has not been submitted for any other degree.

Patricia A. Chambers

St. Andrews, February 1982

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CONTENTS

SYMBOLS AND ABBREVIATIONS

C	chlorophyll *a* concentration ($\mu g\ l^{-1}$)
θ_C	temperature in degrees Centigrade
cm	centimetres
CO_2	carbon dioxide
e	base of the natural logarithm
exp	exponent
F	fraction of the total subsurface light attenuated by chlorophyll *a*
FR	far red light (730 $\pm$ 6.5nm)
g	grams
GF/C	Whatman glass fibre filter paper, grade C
GMT	Greenwich Mean Time
h	hours
I	irradiance
I_{comp}	irradiance where net photosynthesis is zero
I_k	irradiance at which an extrapolation of the initial linear range of a photosynthetic rate-irradiance curve would reach the light saturated rate (Talling 1957a)
I_{max}	irradiance at which P_{max} is attained
K	vertical diffuse attenuation coefficient (ln units m^{-1})
k_c	attenuation coefficient for chlorophyll determined as the average increment in K_R per unit increase in chlorophyll *a* concentration (ln units $mg^{-1}\ m^{-2}$)
K_{FR}	vertical diffuse attenuation coefficient for FR light
$K_{FR(leaf)}$	attenuation coefficient for FR light by *P. crispus* leaves
km	kilometres
K_{PAR}	vertical diffuse attenuation coefficient for PAR
K_R	vertical diffuse attenuation coefficient for R light
K_R/K_{FR}	ratio of the vertical diffuse attenuation coefficients for R and FR light
$K_{R(leaf)}$	attenuation coefficient for R light by *P. crispus* leaves
k_w	attenuation coefficient for water and nonchlorophyll, light-absorbing compounds (ln units m^{-1})
l	litres
ln	natural logarithm
m	metres
mg	milligrams
mM	millimoles per litre
N	north latitude
nm	nanometres
O_2	oxygen

p	probability
P	gross photosynthetic rate
PAR	photosynthetically active radiation (400-700nm)
Pfr	FR-absorbing form of phytochrome
pH	measure of the average proton free energy per proton
P_{max}	saturating gross photosynthetic rate
Pr	R-absorbing form of phytochrome
Ptotal	total amount of phytochrome
r	correlation coefficient
R	red light (660 $\pm$ 5.8nm)
s	seconds
S	south latitude
SCUBA	Self Contained Underwater Breathing Apparatus
S.E.	standard error
tan h	hyperbolic tangent
w	watts
W	west longitude
α	slope of the initial linear range of the photosynthetic rate-irradiance curve at low PAR photon fluence rates
δ^2	index of goodness of fit
ζ	ratio of the R to FR photon fluence rates
ζ_c	average increment in ζ per unit increase of algal biomass
φ	photostationary equilibrium expressed as the ratio of Pfr to Ptotal
µg	micrograms

CHAPTER 1

INTRODUCTION

In cool temperate climates most aquatic angiosperms which neither persist in a vegetative state throughout the year nor perennate by rhizomes, rootstalks or tubers, produce turions, specialized vegetative buds which can function as both propagules and overwintering organs (Glück 1906). They vary in complexity from merely a thickened frond in Spirodela polyrrhiza (Jacobs 1947) and condensed apices in species such as Ceratophyllum demersum and Elodea canadensis (Sculthorpe 1967), to the highly modified and very distinctive forms produced by Utricularia vulgaris (Winston and Gorham 1979) and Hydrocharis morsus-ranae (Sculthorpe 1967). Despite their morphological variability, all turions are characterized by a short shoot axis enclosed by young leaves or scales (Glück 1906).

The induction of dormancy in aquatic angiosperms has been studied much less than in woody plants. Prior to the experimental work of Glück (1906), turions were regarded as strictly overwintering organs produced by annual aquatic angiosperms in response to an endogenous developmental rhythm. However, it became clear that turion production actually represents an adaptive strategy to conditions unfavourable to active vegetative growth (Sculthorpe 1967). Thus, autumnal turion production, typical of most temperate climate aquatic angiosperms, is usually initiated in response to diminishing photoperiods, often in association with low temperatures. Dormancy induction by short days has been shown to occur in Hydrocharis morsus-ranae (Vegis 1953),

Pinguicula grandiflora (Heslop-Harrison 1962), Myriophyllum verticillatum (Weber and Nooden 1974), and Utricularia vulgaris (Winston and Gorham 1979). Utricularia minor, Myriophyllum verticillatum, and Sagittaria sagittifolia have also been reported to form turions in response to nutrient deficiency (Göebel 1891-1893 and Von Luetzelburg 1910 cited in Arber 1920, Glück 1906).

The genus Potamogeton, the freshwater pondweeds, show an abundant evolution of hibernating buds, representing numerous stages in the transition from dense shoot apices to highly specialized turions (Hagström 1916). In P. coloratus, P. foliosus, P. gemmiparus, P. polygonifolius, and P. vaseyi the turions are merely condensed apices, scarcely different from ordinary young leafy shoots. In other species, such as P. pusillus, P. berchtoldii, P. trichoides, and P. obtusifolius, the turions are produced at the shoot apices and in the leaf axils and consist of closely appressed young leaves enclosed in scales corresponding morphologically to axillary stipules accompanied by rudimentary laminae (Arber 1920). In P. alpinus, P. lucens, and P.xfluitans, the turions are formed chiefly on the rhizome system and the upright dormant apices are enclosed by scales consisting of axillary stipules, the corresponding laminae having entirely disappeared (Arber 1920). The most specialized turions of the entire genus are, undoubtedly, produced by P. crispus. Although exhibiting a wide variety of form, they all have a hard, horny texture and bear three to seven small leaves which stand out at an angle from the thickened, spinuous stem.

In most temperate climate aquatic angiosperms the unfavourable environmental conditions associated with autumn, notably short days, low temperature, and possibly low irradiance, are responsible for turion formation. By contrast, P. crispus is reported to produce turions in the summer and to grow luxuriantly throughout the winter (Sauvageau 1894, Fryer et al. 1915, Nasar and Munshi 1978, Sastroutomo et al. 1979, Sastroutomo 1981, Nicholson 1981). However, not all temperate climate populations of P. crispus produce turions (Sauvageau 1894). Of those which do, the onset of turion formation and the magnitude of turion production is often highly variable, even within a single lake (Sauvageau 1894). Furthermore, the turions of P. crispus have been reported to germinate both in the autumn, only several weeks after abscission (Sauvageau 1894, Sastroutomo et al. 1979, Sastroutomo 1980, 1981) and in the spring, after winter dormancy (Singh 1964). As Rogers and Breen (1980) conclude, "The factors initiating turion development on the mature plant [of P. crispus] are not clear."

The objective of the present study was to investigate the environmental factors inducing summer turion formation in Potamogeton crispus L. Potamogeton obtusifolius Mert. and Koch, a typical temperate climate species which produces turions in the autumn, was studied for comparative purposes. In freshwater lakes, the environmental parameters generally exhibiting seasonal variation and which may, therefore, regulate developmental changes in aquatic plants, are nutrients, temperature, daylength, and the aquatic light climate. Turion production has been reported for plants of P.

crispus grown at both high and low nitrogen and phosphorus concentrations (Mulligan et al. 1976) and thus, nutrient concentration, specifically nitrogen and phosphorus, is unlikely to represent the primary stimulus for dormancy induction. Seasonal changes in temperature and daylength have been shown to initiate the transition from vegetative shoot growth to turion production in many aquatic angiosperms (Vegis 1953, Heslop-Harrison 1962, Weber and Nooden 1974, Winston and Gorham 1979), however none of the previously investigated species exhibit highly sporadic turion production, as reported for P. crispus (Sauvageau 1894). Seasonal variation in underwater light quantity and light quality have rarely been investigated and thus, the influence of these environmental parameters on growth and development of aquatic angiosperms is not fully understood.

In order to identify the environmental parameters initiating turion formation in P. crispus and P. obtusifolius, the phenological development of both species was studied for natural populations growing in two Scottish lakes. The onset of turion formation was compared with seasonal variation in temperature, daylength, underwater light attenuation and light quality, specifically the red and far red wavelength bands.

However, field studies, while serving to identify the environmental factors regulating a particular morphological response, rarely permit controlled manipulation of environmental parameters. Hence, laboratory experiments are usually required in order to validate hypotheses derived from field observations. In this study,

the individual effects of temperature, daylength, light quantity (irradiance) and light quality on the formation of turions in P. crispus and P. obtusifolius were assessed in controlled laboratory experiments. In particular, the mode of action of daylength in regulating dormancy induction was investigated. Through the integration of these field and laboratory studies, a model of phytochrome action in the control of photoperiodic and photomorphogenetic responses of aquatic angiosperms was developed and the role of turions in the life history of P. crispus and P. obtusifolius was assessed.

CHAPTER 2

MATERIALS AND METHODS

2.1 STUDY LAKES

2.1.1 Loch Drumore

Loch Drumore ($56^{o}44'N$ $3^{o}22'W$) was artificially created in the early part of this century and has an area of $0.04km^2$ and a maximum depth of 4.3m. In cross-section, it appears conical, with the greatest depth at the western shore beside the dam. The loch is fed by seven streams and the outflow, in the south-west corner, drains into a bog. Loch Drumore lies in an area of limestone and quartzose mica-schist. It is 350m above sea level and bordered by the Overcraig (550m) on the north and reforested hills (500m) on the south-east. *Elodea canadensis* is the most common macrophyte in the loch. *P. obtusifolius* is found in small scattered beds at the western end and *Potamogeton praelongus* occurs towards the centre of the loch, *P. crispus*, *Littorella*, *Chara*, and *Myriophyllum* are located along the shore. *Carex rostrata* occurs in the eastern end of the loch.

Measurements of light penetration were conducted at three permanent sites (numbered 1, 2 and 3)and three unmarked sites, the latter within a radius of 5m from a permanent marker. Site 1 was located in open water, and sites 2 and 3 were located in open water columns within a dense Elodea canadensis bed. P. obtusifolius was collected from a depth of 3.5m and P. crispus from a depth of 0.5m.

2.1.2 Long Loch

Long Loch (56°32´N 3°9´W) lies in an area of old red sandstone. It is 221m above sea level and is bordered on the west by steep hills (320m above sea level), while the eastern shore is low and wooded. The surface area is 0.28km^2 and the maximum depth is 4.3m (mean depth 3.0m) (Murray and Pullar 1910). The loch forms a simple basin with the maximum depth occurring near the centre of its length, but much nearer the western than the eastern shore.

The study area was located near the centre of the loch´s length, opposite the access road. Measurements of light penetration were made at six sites across the loch and P. crispus was collected from a depth of 2.0m, off the east shore.

2.1.3 Lake of Menteith

The Lake of Menteith (56°10´N 4°18´W) lies in an area of old red sandstone overlain by deposits composed partly of boulder clay. It has a surface area of 2.64km^2 and a maximum depth of 23.5m (mean depth 6.0m) (Murray and Pullar 1910).

P. obtusifolius was collected from a depth of 2.7m to 3.2m between the islands of Inchmahome and Inch Talla.

2.1.4 Fingask Loch

Fingask Loch (56°34´N 3°22´W) lies in an area of old red sandstone and is surrounded by low cultivated land. It has a surface area of 0.16km^2 and a maximum depth of 14.6m (mean depth 7.0m) (Murray and Pullar 1910). The bottom of the loch slopes down gradually on all sides to the deepest part, which is approximately centrally placed. Except for the north-western angle of the loch and along the shoreline, aquatic macrophytes are generally absent.

Measurements of diurnal light penetration were conducted on the east side of the loch, opposite the access road, at depths greater than 3.5m.

2.1.5 Loch Lomond

Loch Lomond consists of two distinct basins, the shallow south basin and the deep north basin (maximum depth 190m) (Murray and Pullar 1910). Measurements of diurnal light penetration were conducted in the north basin on the east side of the loch near Ptarmigan Lodge ($56^{o}11'N$ $4^{o}38'W$). The loch is 7.3m above sea level and its shores are mountainous; to the east of the study site is Ptarmigan (731m) and Ben Lomond (973m) and to the west Ben Reoch (632m) and Beinn Bhreac (742m).

2.2 FIELD MEASUREMENTS

2.2.1 Plant Phenology

Seasonal collections of *P. crispus* and *P. obtusifolius* from Loch Drumore and *P. crispus* from Long Loch were made by wading or using SCUBA (Self-Contained Underwater Breathing Apparatus). On every collection date approximately ten plants of each species were pressed for phenological study.

2.2.2 Light

Underwater light penetration was measured with a Macam Photometrics Limited model Q101-1 quantum radiometer. Three waterproof sensors, each cosine corrected, with spectral responses of 660nm (bandwidth 11.6nm), 730nm (bandwidth 12.9nm), and 400 to 700nm were used to measure photon fluence rates (μmole m^{-2} s^{-1}) of red (R), far red (FR), and photosynthetically active radiation (PAR), respectively. The sensors, fixed in a horizontal position, were lowered down the unshaded side of the boat from an outrigger projecting 75cm over the stern. Measurements were made at half-meter depth intervals from 0.5m below the water surface to 4.5m or the nearest meter above the bottom. In order to correct for variations in solar irradiance, above-surface PAR was measured at each depth interval with a selenium photocell connected to an Avo Limited Electronic avometer type EA113.

Vertical diffuse attenuation coefficients for R, FR, and PAR were calculated by linear regression from the equation:

$$K = \frac{\ln I_o - \ln I_z}{z}$$

where K is the vertical diffuse attenuation coefficient (in ln units m^{-1}), I_o is the extrapolated subsurface fluence rate, and I_z is the fluence rate at depth z. The ratio of the R to FR photon fluence rates (ζ, Greek zeta) was also calculated for each depth.

Seasonal profiles of light penetration were measured at three permanent sites and three unmarked sites in Loch Drumore and at a total of six unmarked sites from three depth classes (water columns less than 2.5m deep, from 2.5m to 4.0m deep, and greater than 4.5m deep) in Long Loch. (Occasionally adverse weather conditions reduced the number of profiles measured.) Measurements were conducted between 11.00 and 14.30 GMT.

Diurnal profiles of light penetration were measured at three permanent sites in Loch Drumore, and at four unmarked sites from both Fingask Loch and Loch Lomond. Diurnal measurements of ζ at 0.5m above the water surface were also recorded for Lochs Lomond and Fingask.

2.1 Temperature

Temperature was measured with a thermometer at P. crispus sites in Lochs Drumore and Long, and at the P. obtusifolius site in Loch Drumore by wading or using SCUBA.

2.2.4 Chlorophyll a and Gelbstoff Concentrations

Depth-integrated water samples were collected at each site in Loch Drumore and Long Loch in conjunction with seasonal light penetration measurements for the last six sampling dates. Rigid plastic tubing, 3.0cm in diameter, was lowered through the profile from the water surface to 4.5m or the nearest meter above the bottom, stoppered, raised to the surface and the contents collected.

A surface water sample was collected in conjunction with each diurnal excursion.

Chlorophyll a concentration was estimated from 11 water samples which were filtered through GF/C glass fibre filter paper and extracted into cold 90 percent aqueous acetone for 24 hours at $4^{o}C$. Optical densities of centrifuged extracts were measured at 665nm and 750nm on a Unicam SP600 spectrophotometer with a 1cm pathlength. Chlorophyll a concentration (C), expressed as $\mu g\ l^{-1}$ was calculated from the formula of Talling et al. (in press):

$$C = \frac{[11.9 - (A_{665} - A_{750})] \times v \times 1000}{V \times d}$$

where A_{665} and A_{750} are the absorbances at 665nm and 750nm, respectively, v is the volume of the extract (ml), V is the volume of the original water sample (ml), and d is the pathlength of the spectrophotometer cell (cm).

Gelbstoff concentration was estimated spectrophotometrically by measuring the absorbance of the filtered water at 450nm with a 1cm pathlength.

2.2.5 Statistical Methods

The seasonal light (K_{PAR}, K_R, K_{FR}, K_R/K_{FR}, ζ), chlorophyll, and gelbstoff data were analyzed, in turn, by two-way analysis of variance in order to ascertain the variability between collection sites (or depth classes) and between collection dates. The relationship between K_R and chlorophyll *a* and/or gelbstoff concentration was analyzed by linear regression.

Variations within the diurnal light data (K_{PAR}, K_R, K_{FR}, K_R/K_{FR}, ζ) were analyzed by analysis of variance, followed by Duncans Multiple Range Test, a multiple comparison of means test for determining which comparisons among means are significantly different.

Data are presented in graphs or tables after the appropriate chapters.

2.3 LABORATORY EXPERIMENTS

2.3.1 Photosynthetic Activity

P. crispus and P. obtusifolius were collected from Loch Drumore on 3 August, 15 August, and 21 September, 1980. (The water temperature was approximately 15°C.) Photosynthetic activity was measured immediately upon return to the laboratory according to the procedure of and in the apparatus described by Allen and Spence (1981), through the continuous recording of oxygen concentration in the bathing solution. The apical 8cm of one shoot (P. crispus) or apical 4cm of four shoots (P. obtusifolius) were placed in the cuvette (modified by the removal of the pH electrode side-arm) in a 1mM bicarbonate solution at 15°C. Oxygen concentration was measured by a Beckman Instruments 39553 Oxygen Sensor connected to a Beckman Fieldlab oxygen meter and was recorded on a strip chart recorder. The rate of oxygen production was determined from the slope of the trace.

Irradiance was provided by two 250w reflector incandescent lamps and the PAR photon fluence rate, measured inside the cuvette by the quantum radiometer described earlier, was adjusted by neutral density filters. Rate-irradiance curves were produced by increasing the PAR fluence rate until the plant attained saturation, followed by a return to the lowest irradiance and then to total darkness. Three curves were produced for each species on each date. Plants were dried at

80°C to a constant weight.

The data were analyzed by analysis of variance.

2.3.2 Growth Control Experiments - P. crispus

P. crispus was collected from Loch Drumore and a length of rhizome, bearing two to five shoots, was potted in lake sediment, overlain with sand. Plants were grown in tap water under conditions of low temperature (less than 15°C) and short days (less than 10h) for a minimum of two weeks prior to experimentation.

At the start of each experiment, the number of shoots in each pot was recorded. Plants were observed daily for appearance of first turion. (Turions were harvested when observed.) Thereafter, the number of shoots and turions per pot were recorded, usually twice each week. Experiments were terminated on day 35. The results are expressed as the turion index (the total number of turions divided by the mean number of shoots for each pot) and the number of days until appearance of the first turion. Data are presented in graphs or tables after the appropriate chapters.

Experiments were conducted to determine the individual roles of temperature, photoperiod, PAR photon fluence rate, and ζ on turion production. All treatments were evaluated against a control in which the temperature was 30°C, the photoperiod was 18h, the PAR photon

fluence rate was 400μmole m^{-2} s^{-1}, and ζ was 12. In each experiment, one environmental parameter was varied; the other three remained constant as per the control. Irradiance was provided by the following lighting systems, as determined by ζ :

ζ = 0.9 3-250w reflector incandescent lamps

ζ = 2.3 { 7-40w white fluorescent lights
7-60w incandescent lamps

ζ =12 6-40w white fluorescent lamps

ζ =24 { 4-40w white fluorescent lamps
2-40w grolux fluorescent lamps

PAR was reduced from the control value of 400μmole m^{-2} s^{-1} to 60 or 100μmole m^{-2} s^{-1} for the experimental treatments by neutral density filters. Temperatures were maintained at 30°C for the control and at 15, 20, 25, or 35°C±2°C for the experimental treatments by Techne TE-7 thermoregulators and Techne RU-2 dip coolers. Photoperiod was 18h for the control and 10, 12, 16, 18, or 24h for the experimental treatments.

The minimum number of inductive days required for turion formation was determined by pretreatment under an 18h photoperiod at 30°C for 0 to 5 days followed by transference to short days (10h) at 30°C, short days (10h) at 15°C, or long days (18h) at 15°C. The PAR photon fluence rate was 400μmole m^{-2} s^{-1} and ζ was 12 for all conditions.

To investigate the mode of action of daylength on turion production, individual pots were enclosed in plastic bags containing tap water or sucrose solution (0.3, 0.6, or 3.0mM) and placed in 30°C water baths such that the tops of the bags remained above the water surface. Plants were grown under:

1. short days (10 or 12h photoperiod, 400μmole m^{-2} s^{-1} PAR, ζ value of 12),
2. short days with a one hour dim R night-break during the middle of the dark period, or
3. short days with an 8h dim R or FR end-of-day extension.

R light (ζ=41) or FR light (ζ=1.0) were provided by grolux fluorescent lamps or incandescent lamps, respectively. The bathing solutions were renewed every three days and the bags were replaced every six days.

2.3.3 Growth Control Experiments - P. obtusifolius

P. obtusifolius was collected from the Lake of Menteith on 17 May, 1981 and individual shoots were potted in lake sediment, overlain with sand. Plants were grown in tap water under conditions of low temperature (less than 15°C) and long days (greater than 16h) for a minimum of two weeks prior to experimentation.

A pilot experiment was conducted to analyze the roles of photoperiod and temperature in turion production. Four treatments, combining either long days (18h) or short days (10h) with either a high (25°C) or low (15°C) temperature, were observed for appearance of turions. The PAR photon fluence rate for all treatments was 200µmole m^{-2} s^{-1} and ζ was 12.

SECTION I

FIELD STUDIES

CHAPTER 3

SEASONAL PHENOLOGY

3.1 INTRODUCTION

In cool temperate climates, most aquatic angiosperms exhibit an annual habit, whereby growth commences in the spring with turion germination and ceases in the autumn with the production of turions. The subsequent death of the parent plant realizes the role of the turions as perennating organs. This annual habit is characteristic of Potamogeton pectinatus (Westlake 1963), Spirodela polyrrhiza (Perry and Byrne 1969), Myriophyllum verticillatum (Weber 1972), Myriophyllum exalbescens (Weber and Nooden 1974, 1976b), Ceratophyllum demersum (Best 1979), Potamogeton zosteriformis (Haag 1979), and Utricularia vulgaris (Winston and Gorham 1979).

In contrast, P. crispus is reported to grow luxuriantly throughout the winter and to produce turions in the summer (Sauvageau 1894, Fryer et al. 1915, Nasar and Munshi 1978, Sastroutomo et al. 1979, Nicholson 1981, Sastroutomo 1981). In order to understand the life cycle of P. crispus and to enable comparisons with other temperate climate macrophytes, the seasonal phenology of P. crispus plants from a natural population was examined, with particular emphasis on turion formation. P. obtusifolius , a typical annual species growing in the same lake, was studied for comparative

purposes.

3.2 RESULTS

Stages in the development of P. obtusifolius are shown in Plates 3.1 to 3.4 for plants collected from Loch Drumore during 1980. Turion germination occurred in the early spring and was characterized by stem elongation at right angles to the long axis and root development (Plate 3.1). In this population, very few plants appeared to germinate from seed and there was no rhizomatous propagation. By late spring, most of the turions had developed well-formed shoots and roots (Plate 3.2). Flowers were produced in the beginning of August by a few plants and immature turions were first observed on 15 August (Plate 3.3). By early autumn well-developed turions, produced at the shoot apices and in the axils of leaves, were observed on all plants (Plate 3.4). The decomposition of the parent plants in late autumn released the turions, which sank to the lake bottom and remained dormant until the following spring.

The yearly cycle of percent composition by each of four arbitrary shoot length classes is illustrated in Fig. 3.1 for P. obtusifolius. The spring population was composed of predominantly short shoots (less than 20cm) which were replaced by progressively longer shoots during the summer and autumn months. Additional short shoots were not produced, confirming the observation that the entire population was initiated in the spring.

Stages in the development of P. crispus are shown in Plates 3.5 to 3.8 for plants collected from Loch Drumore during 1979 and 1980. (Similar developmental stages were observed in the P. crispus population in Long Loch.) Turions were produced during the summer and germinated in the autumn (Plate 3.5). Stem extension was not observed: instead, lateral shoots developed from axillary buds of the turion and produced either rhizomes or erect leafy shoots (Plate 3.6). During the winter and spring, extensive production of new shoots, through vegetative propagation of the rhizome, was observed. The leaves of these shoots were flat, with a finely serrulate margin, and bright green in colour (Plate 3.7). During the summer, fewer shoots were initiated and the existing shoots produced new leaves which were often red-green in colour with a crisped or undulate margin. Flowers were never produced in these populations. Turions were first observed on 5 June 1980 and during the following 10 weeks, 34 turions were produced (Plate 3.8). Of the 70 shoots collected during this period, 19 percent bore turions. After abscission of the turions, the parent plant usually died.

The yearly cycle of percent composition by each of four arbitrary shoot length classes is illustrated in Fig. 3.2 for P. crispus from Loch Drumore. In September 1979 short shoots (less than 10cm) comprised less than 15 percent of the total population. However, by October and throughout the winter and spring, these short shoots represented about 50 percent of the population and were probably initiated from turions and by vegetative propagation of the rhizome. Almost the entire winter and spring populations had shoot lengths of

less than 20cm, possibly controlled by low temperatures, reduced PAR, and the scouring effect of up to 15cm of ice. From May to September shoots less than 10cm high comprised less than 20 percent of the population, and there was a progressive increase in shoot length. P. crispus appears to produce new shoots during winter and spring and these shoots mature during the summer months.

3.3 DISCUSSION

The life cycle of P. obtusifolius is typical of a temperate climate aquatic angiosperm. Growth is initiated in the spring from turions produced the previous autumn; seedlings are rarely observed, although anthesis occurs each summer. Maximal biomass is attained during the summer months and the turions, initiated in the late summer or early autumn and released by late autumn, enter a state of innate dormancy that persists until spring (Weber and Nooden 1974, Aiken and Walz 1979, Winston and Gorham 1979). A schematic diagram of the developmental stages of P. obtusifolius is presented in Fig. 3.3.

In contrast to many temperate climate aquatic angiosperms, P. crispus is a wintergreen species. Turion germination occurs in the autumn and maximum biomass is attained in the early spring through turion and rhizome propagation (Fryer et al. 1915, Nasar and Munshi 1978, Sastroutomo et al. 1979, Rogers and Breen 1980, Sastroutomo 1980, 1981). Although the populations studied here did not flower, anthesis has been observed in P. crispus (Hunt and Luntz 1959,

Sastroutomo et al. 1979, Rogers and Breen 1980), however seed germination is low (Waisel 1971). Rogers and Breen (1980) reported that in a natural population of P. crispus, 1445 seeds and 1129 turions were produced per square meter but only 0.001 percent of the seeds, in contrast to 60 percent of the turions, germinated.

Turion production in P. crispus is initiated around midsummer. After abscission of the turions several weeks later, the parent plants die and the population reaches its minimum yearly biomass (Sauvageau 1894, Mulligan et al. 1976, Sastroutomo 1980, 1981, Nicholson 1981). The abscised turions enter a period of imposed dormancy, in response to high temperatures, which persists until the decreased temperatures of autumn permit germination (Waisel 1971, Rogers and Breen 1980, Sastroutomo 1981). Figure 3.4 illustrates the stages of development for P. crispus.

The difference between `spring´ and `summer´ leaves in P. crispus is also indicated Fig. 3.4, although the populations observed here never produced the strongly crisped leaves characteristic of the species. The flat-leaved form was originally classified as P. serratus by Hudson (1862 cited in Fryer et al. 1915), however this form is now considered to represent P. crispus in the young state or when grown in crowded conditions (Fryer et al. 1915).

The large morphological variability shown by P. crispus turions has long been recognized (Sauvageau 1894, Hagström 1916, Sastroutomo 1980) although, as yet, there is no predicting for a single plant at which, of a number of possible sites, turions will be produced or on

their form. Sauvageau (1894) recognized three main types of turions:

1. small turions with leaves having a short thickened base and a long terminal `foliage´ end, and which often develop in the shoot axils (Fig. 3.4a),
2. very thin turions, often several centimetres long, with a rectilinear or zig-zag axis, long internodes and leaves that are short and narrow, and which are often produced at the apex of vegetative shoots (Fig. 3.4b), and
3. large turions with five to 10 compressed, thick internodes, and short, horny leaves, and which often develop on flowering shoots (Fig. 3.4c).

Very few turions of the latter type were observed in the Loch Drumore and Long Loch populations, as these plants failed to produce flowers.

P. obtusifolius is the ideal example of a temperate climate aquatic angiosperm. The turions of P. obtusifolius, produced in the autumn and released after the death of the parent plant, function primarily as perennating organs. In P. crispus, however, the rhizome system persists throughout the year. The turions do not serve as overwintering devices, for maximum productivity occurs during this season. Instead, they germinate in the autumn, only two months after abscission, producing as many as six or seven independent shoots or rhizome systems. Thus, the turions of P. crispus may function primarily as propagules. However, in order to fully evaluate the importance of turions in the life history of P. crispus, the environmental parameters controlling turion production must be determined.

Plate 3.1. Turions of P. obtusifolius collected from Loch Drumore in April 1980. The four upper turions show stem elongation, characteristic of germination. (Scale: centimetres)

Plate 3.2. Plants of P. obtusifolius collected from Loch Drumore in May 1980. (Scale: centimetres)

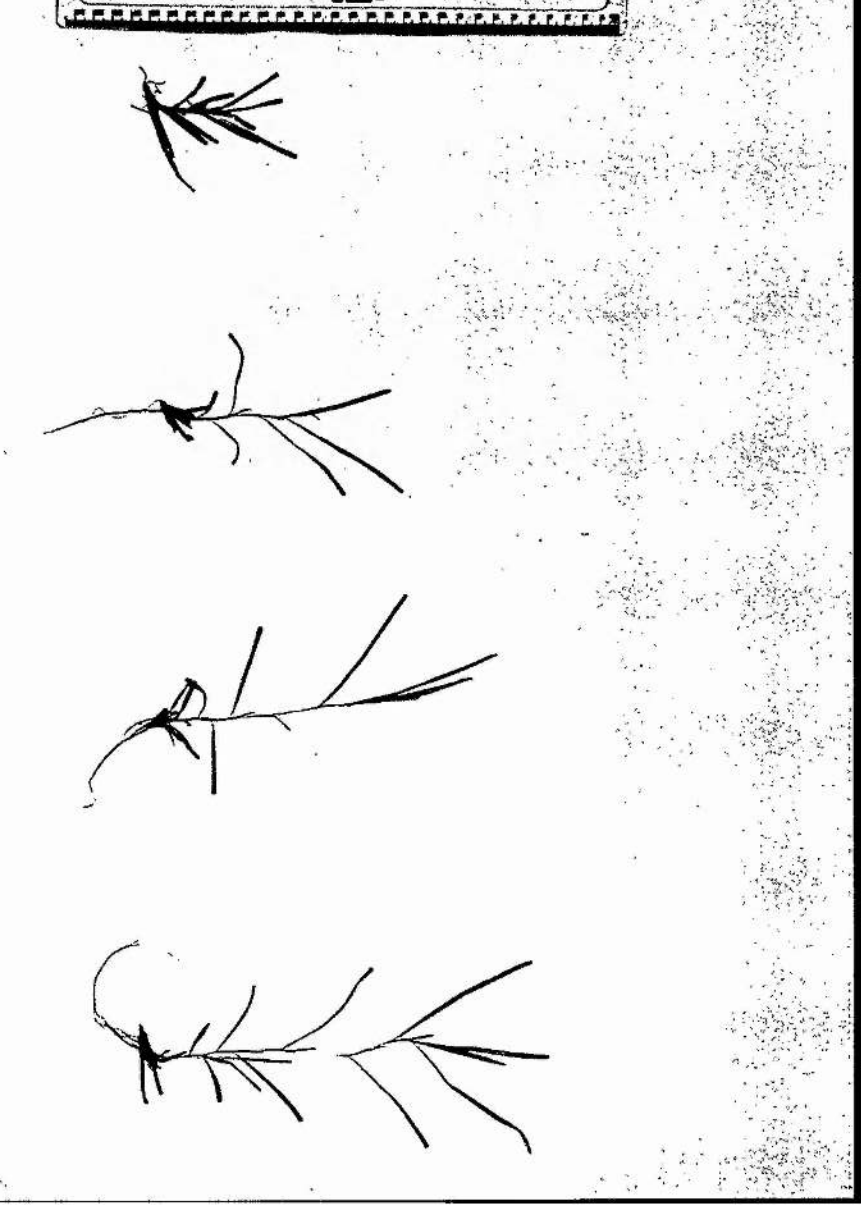


Plate 3.3. Plants of P. obtusifolius collected from Loch Drumore in August 1980. The shoot on the far right is flowering and also bears immature turions. (Scale: centimetres)

Plate 3.4. Plants of P. obtusifolius collected from Loch Drumore in September 1980. Turions are present on all shoots. (Scale: centimetres)

Fig. 3.1. Monthly changes in the percentage of plants of P. obtusifolius in each of four arbitrary shoot length classes during 1980. (a) 0-20cm, (b) 21-40cm, (c) 41-60cm, (d) greater than 61cm.

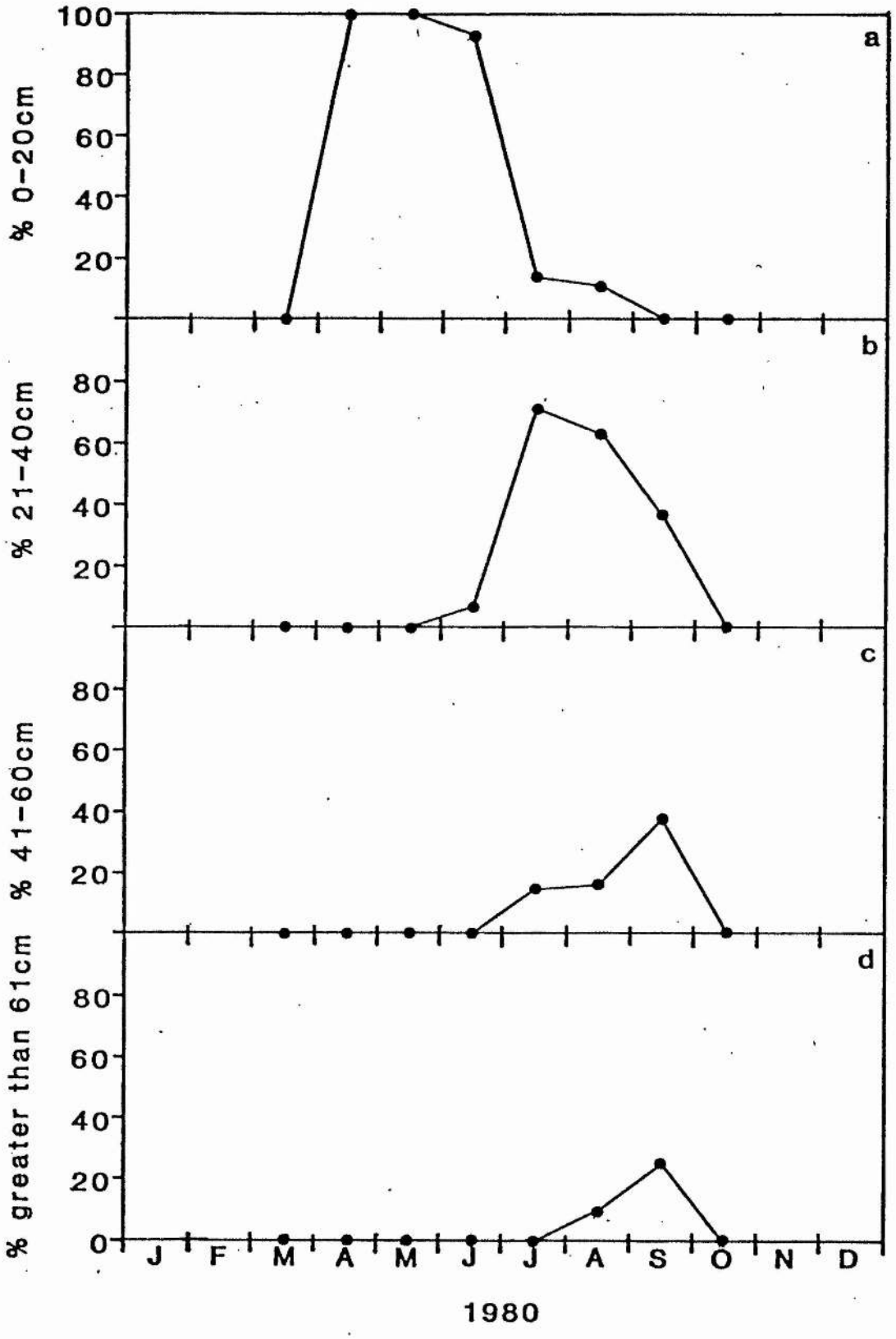

% 0-20cm
% 21-40cm
% 41-60cm
% greater than 61cm
a
b
c
d
100
80
60
40
20
0
J
F
M
A
M
J
J
A
S
O
N
D
1980

Plate 3.5. Turions of P. crispus collected from Loch Drumore in August 1979. (Scale: centimetres)

Plate 3.6. Plants of P. crispus collected from Loch Drumore in November 1979. The second plant from the right is still attached to the turion from which it germinated. (Scale: centimetres)

Plate 3.7. Plants of P. crispus collected from Loch Drumore in May 1980. (Scale: centimetres)

Plate 3.8. Plants of P. crispus collected from Loch Drumore in July 1980. The first, second and fourth plants from the left bear axillary turions. (Scale: centimetres)

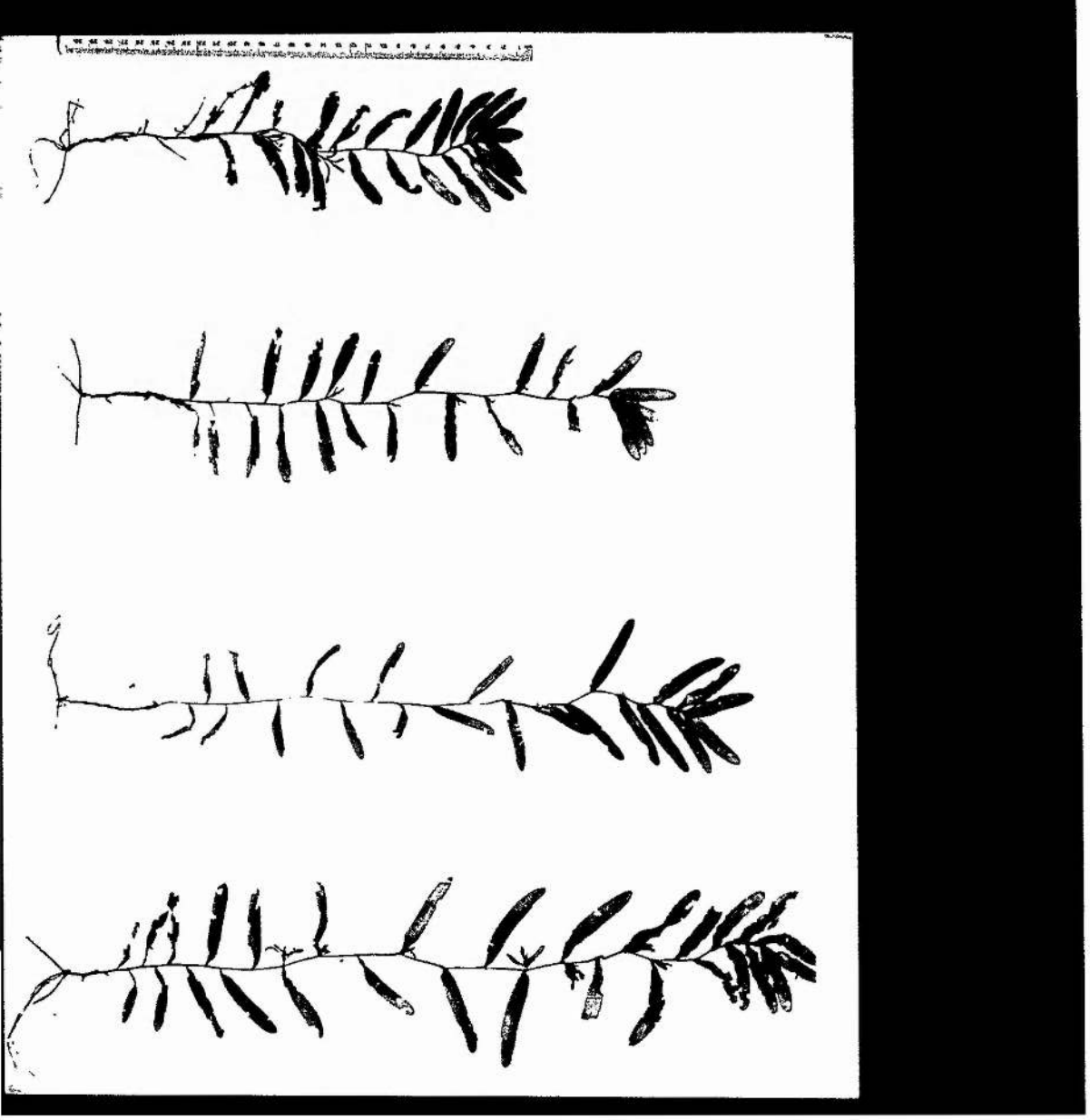
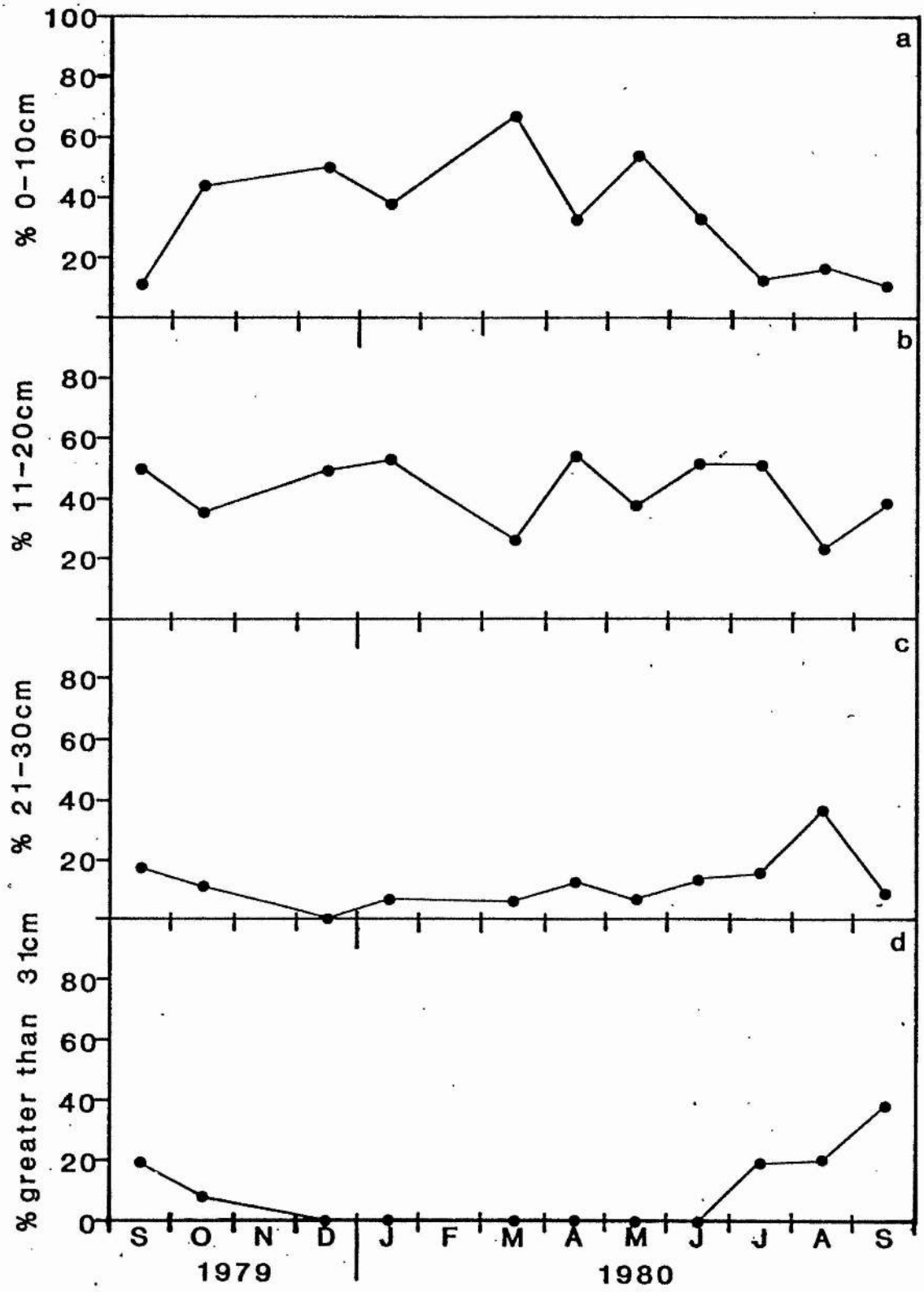


Fig. 3.2. Monthly changes in the percentage of plants of P. crispus in each of four arbitrary shoot length classes collected from Loch Drumore from September 1979 to September 1980. (a) 0-10cm, (b) 11-20cm, (c) 21-30cm, (d) greater than 31cm.


a
% 0-10cm
100
80
60
40
20
b
% 11-20cm
80
60
40
20
c
% 21-30cm
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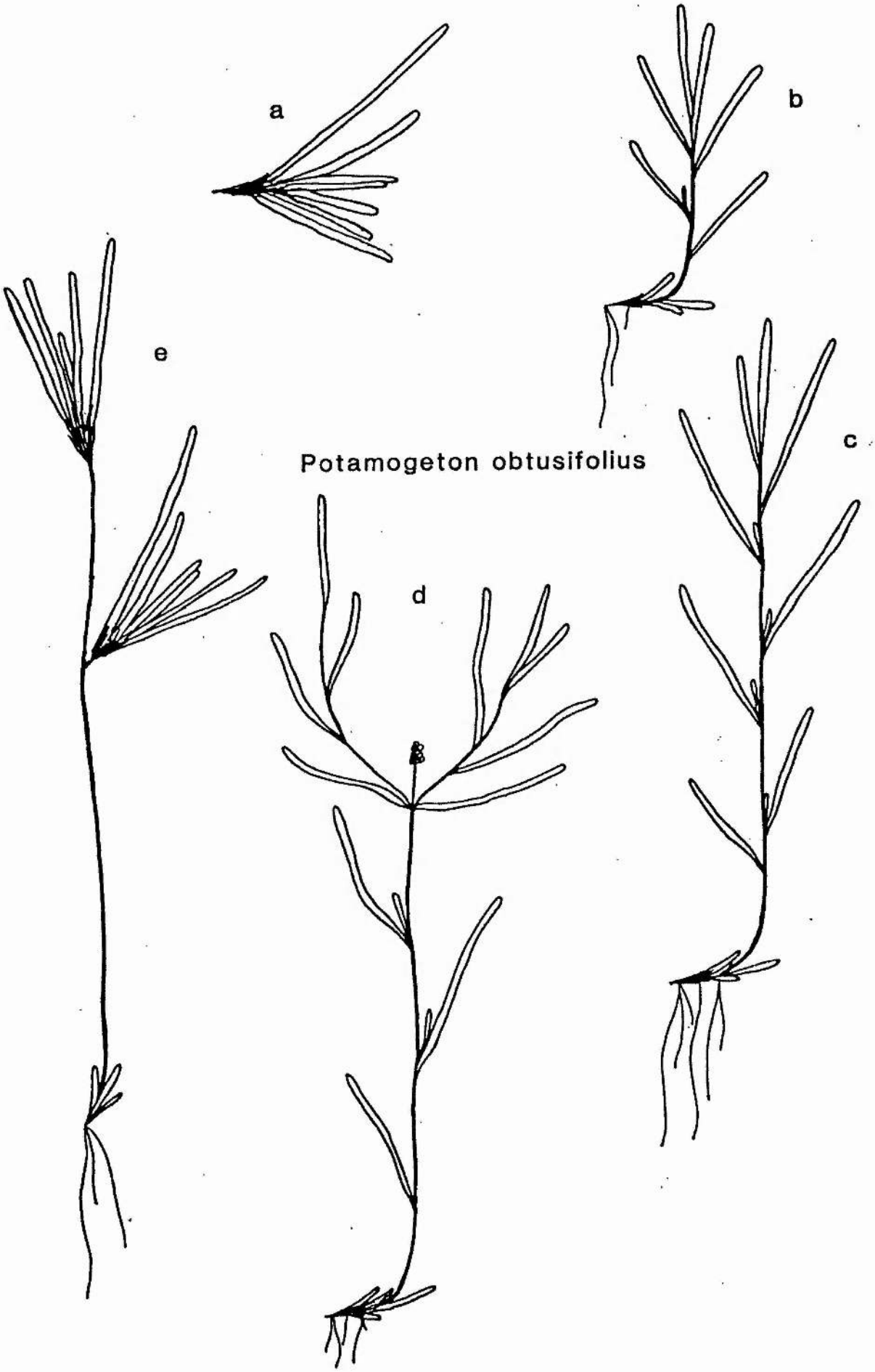
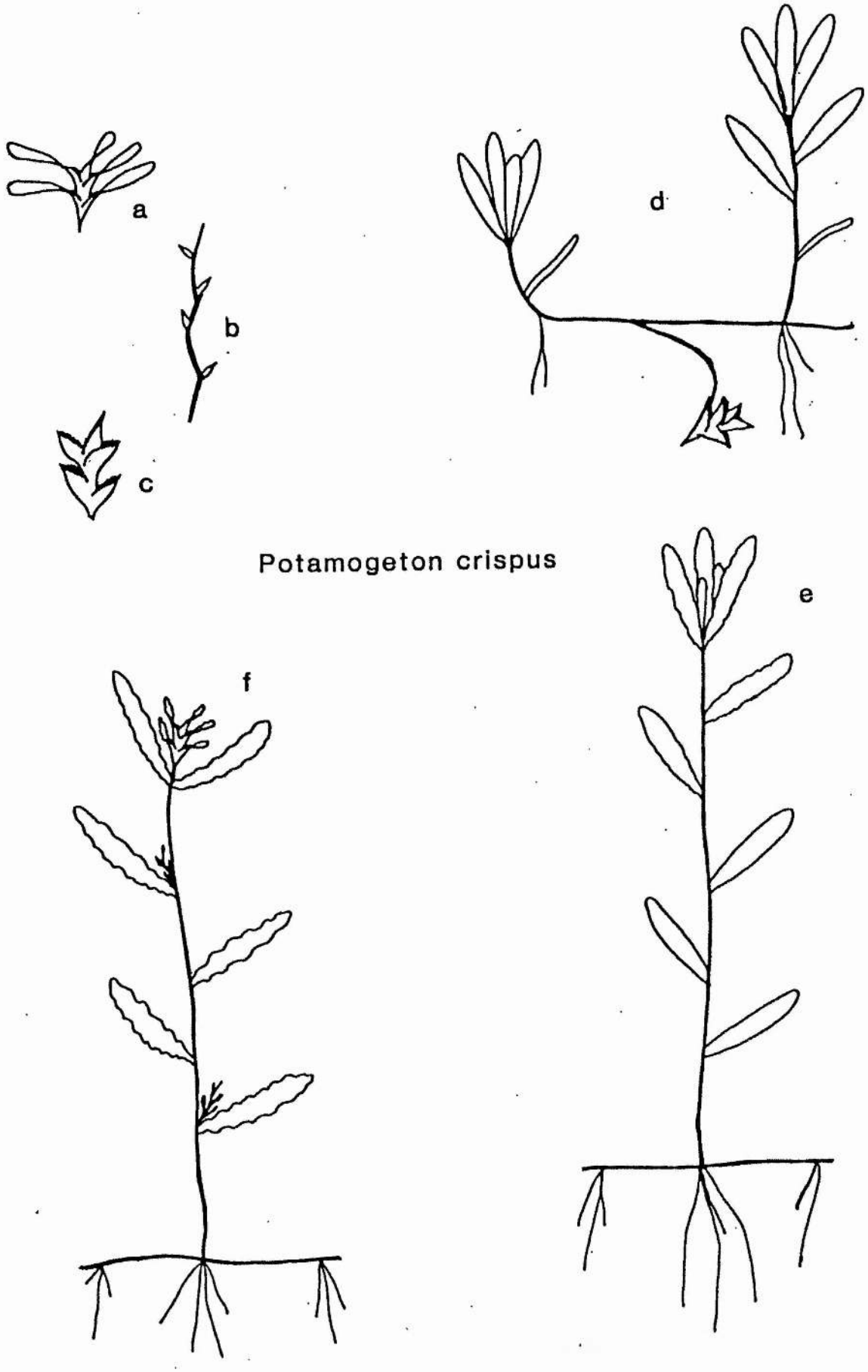
60
40
20
d
% greater than 31cm
80
60
40
20
0
S
O
N
D
J
F
M
A
M
J
J
A
S
1979
1980

Fig. 3.3. Developmental stages in the life cycle of P. obtusifolius. (a) ungerminated turion, (b) germinating turion, (c) vegetative shoot, (d) flowering shoot, (e) shoot bearing mature turions. (Not to scale.)



Potamogeton obtusifolius

Fig. 3.4. Developmental stages in the life cycle of P. crispus. (a), (b), (c) ungerminated turions, (d) rhizome system and shoots produced by turion, (e) vegetative shoot, (f) shoot with `crisped´ leaves and bearing two axillary and one apical turion.



Potamogeton crispus

CHAPTER 4

SEASONAL VARIATION IN THE AQUATIC ENVIRONMENT

4.1 INTRODUCTION

Turion formation has been observed in natural populations of *P. crispus* only during midsummer and in *P. obtusifolius* only during late summer and early autumn. Such strictly seasonal behaviour suggests that turion formation may be triggered by one or more environmental factors which undergo predictable seasonal change. In freshwater lakes, nutrient supply, temperature, and the light climate may exhibit regular seasonal cycles. Competition for a limited nutrient supply, in particular nitrogen and phosphorus, becomes more intense during the summer months when increased temperatures promote rapid growth of both submerged macrophyte and phytoplankton populations. The underwater light climate may also exhibit seasonal variation in light quantity (irradiance), light quality (particularly the R and FR wavelength bands), and photoperiod. In temperate climate terrestrial systems, the PAR photon fluence rate and ζ values on a woodland floor have been found to change in a predictable manner throughout the year and the magnitude of the ζ change is sufficient to provide a stimulus which may be of importance in the determination of growth pattern (Tasker and Smith 1977). Seasonal changes in light penetration and ζ in the underwater environment have yet to be investigated and thus their role in the control of growth of aquatic angiosperms is not fully understood.

Although turion formation may be induced by an endogenous developmental rhythm, the occurrence of turions on both fruiting and non-fruiting plants in both P. crispus and P. obtusifolius tends to discount this hypothesis. Nitrogen and phosphorus availability is also unlikely to trigger turion formation in P. crispus, as turions were produced by plants grown in outdoor tanks under conditions ranging from no fertilization to high fertilization (5mgN l^{-1}, 0.5mgP l^{-1}) (Mulligan et al. 1976). The objective of the present study was to investigate the seasonal variability in light quantity, light quality, particularly the R and FR wavelength bands, photoperiod and temperature in order to identify the environmental variables triggering turion formation in P. crispus and P. obtusifolius.

4.2 RESULTS

4.2.1 Seasonal Light Climate

Figure 4.1 illustrates the seasonal variation in underwater light attenuation for Long Loch. Attenuation of PAR, R and FR radiation differed significantly ($p < 0.01$) between the three depth classes (less than 2.5m, between 2.5m to 4.5m inclusive, and greater than 4.5m) on a single day. A relatively constant relation was observed between the

sites, with maximum attenuation of K_{PAR}, K_R, and K_{FR} always occurring in the shallow water.

Each of the three depth classes also showed significant seasonal variation ($p<0.01$) in K_{PAR}, K_R, and K_{FR} with maximal attenuation occurring during the summer.

While both K_R and K_{FR} were significantly different ($p<0.01$) between the three depth classes on a single day, the ratio of K_R to K_{FR} (K_R/K_{FR}) and ζ for a given depth were not significantly different between depth classes ($p>0.05$) although there was significant ($p<0.01$) seasonal variation (Fig. 4.2).

Underwater light attenuation in Loch Drumore presents a much more complex picture (Fig. 4.3). On a single day, K_{PAR}, K_R, and K_{FR} were highly variable between the marked sites, however no one site exhibited consistently higher or lower attenuation in the three spectral regions. In contrast to Long Loch, where aquatic macrophytes were entirely absent from the sites of light measurement, sites 2 and 3 in Loch Drumore were located in open water columns of small diameter within a dense bed of Elodea canadensis. Site 1 was located in open water.

Each of the three marked sites also showed significant ($p<0.05$) seasonal variation in K_{PAR}, K_R, and K_{FR}. As in Long Loch, K_R/K_{FR} and ζ for a given depth were not significantly different ($p>0.05$) between sites on a single day, although seasonal variation was significant ($p<0.05$) (Fig. 4.4).

To further assess the variability in light attenuation within open water columns of continuous vegetation, seasonal measurements of K_{PAR}, K_R, and K_{FR} were conducted at each of three unmarked open-water sites within a Potamogeton praelongus/Elodea canadensis bed (Fig. 4.5). Attenuation of the three spectral regions was usually highly variable between the sites on a single day.

The correlation coefficients (r) from the determinations of K (the linear regression of the natural logarithms of the photon fluence rate on depth) were always greater than 0.94. Thus, the variability between sites and between dates cannot be attributed to unreliable attenuation coefficients caused by horizontal stratification of attenuating particles through the water columns.

4.2.2 Factors Affecting Light Attenuation

For the last six sampling dates (April to August 1981), chlorophyll a ($\mu g\ l^{-1}$) and gelbstoff concentrations were measured in conjunction with diffuse light attenuation for the three depth classes in Long Loch and the three marked sites in Loch Drumore. Figure 4.6 shows the day-to-day variation in chlorophyll a concentration, gelbstoff concentration, and light attenuation for a representative depth class from Long Loch. K_{PAR}, K_R, K_{FR}, and K_R/K_{FR} were significantly different between the dates ($p<0.01$) and, with the exception of K_R/K_{FR}, between depth classes ($p<0.01$). Gelbstoff and

phytoplankton concentrations were also significantly different ($p<0.01$) between dates, however gelbstoff concentration, unlike phytoplankton concentration, was not significantly different between depth classes ($p>0.05$).

Low phytoplankton and gelbstoff concentrations correlated with increased light penetration in each of the three spectral regions and with maximal ζ values for any depth. At high chlorophyll a and gelbstoff concentrations, light penetration was reduced and ζ approached equality for all depths.

The seasonal variation in K_R in Long Loch shows a positive correlation to changes in phytoplankton concentration (Fig. 4.7). The slope of the regression line, 0.018, represents the mean spectral attenuation coefficient for chlorophyll (k_c) in ln units mg^{-1} chlorophyll a m^{-2}, as originally defined by Talling (1960b). The attenuation coefficient for water and nonchlorophyll, light-absorbing compounds (k_w), indicated in Fig. 4.7 by the intercept of the regression line on the y-axis, is 0.68 ln units m^{-1}. Multiple linear regression of gelbstoff concentration on phytoplankton concentration and light attenuation did not produce a substantially higher correlation coefficient ($r=0.88$).

Figure 4.8 shows the day-to-day variation in gelbstoff concentration, chlorophyll a concentration, and light attenuation at the open water site in Loch Drumore. K_{PAR}, K_R, K_{FR}, and K_R/K_{FR} at each of the three marked sites were significantly different between the dates April to August 1981 ($p<0.01$). Gelbstoff and phytoplankton

concentrations also showed significant day-to-day variation ($p<0.01$), however there was no obvious correlation between chlorophyll a concentration and light attenuation. At the low phytoplankton concentrations recorded, the attenuation of light in the red spectral region can not be directly attributed to chlorophyll concentration, as shown in Fig. 4.9, nor can it be correlated with the multiple interaction of gelbstoff and chlorophyll a concentrations ($r=0.23$).

4.2.3 Seasonal Changes in Temperature and Photoperiod

Figures 4.10 and 4.11 illustrate the seasonal changes in temperature recorded for Long Loch and Loch Drumore, respectively. Temperature stratification was observed in neither Loch Drumore nor Long Loch (down to a depth of 3m). The maximum temperature recorded in Loch Drumore was 18.5°C and in Long Loch was 17.0°C.

The seasonal photoperiodic data were obtained from the Nautical Almanac and Astronomical Ephemeris (1944).

4.2.4 Turion Production in P. crispus and P. obtusifolius

Turions were observed on P. crispus in Long Loch from 28 June to 15 August 1980 and in Loch Drumore from 6 June to 15 August 1980. There was no apparent correlation between the time of turion production and light penetration. In Long Loch, turions were produced during the time of both maximal and minimal yearly light attenuation by each of the three spectral classes (Fig. 4.1) and over a range in ζ for a depth of 1.5m (mean depth of shoot apices) from 2.00, the yearly minimum, to 4.36, the yearly maximum (Fig. 4.2). In Loch Drumore, light penetration was not measured at the P. crispus site and the data collected from other sites in the lake revealed that there was considerable variation in the aquatic light climate at any one time. However, in both Long Loch and Loch Drumore, turion production by P. crispus coincided with maximum yearly temperatures and photoperiods (Figures 4.10 and 4.11).

Unlike P. crispus, P. obtusifolius produces only one crop of turions each year and these were first visible on 15 August 1980 in Loch Drumore. The onset of turion production bore no apparent relation to light attenuation as concurrent initiation of turions was observed in plants growing at every site, all of which showed different coefficients of attenuation for the three spectral regions (Figures 4.3 and 4.4). However, turion formation in P. obtusifolius coincided with high summer temperatures and decreasing photoperiods (Figure 4.11).

4.3 DISCUSSION

The attenuation of light in natural waters is determined by a complex interaction of environmental factors, including both the spectral composition of the incident light, and the scattering and absorption properties of the water. The attenuating components of natural waters can be catagorized into four main groups:

1. the water, itself, which preferentially absorbs the longer wavelengths and scatters the shorter wavelengths,
2. gelbstoff, a complex mixture of dissolved and/or colloidal breakdown products, consisting mainly of polymerized oxidized phenolic compounds (Christman and Ghassemi 1966, Hall and Lee 1974), which absorb mainly in the blue and ultraviolet and show selective molecular scattering,
3. non-living particulate matter (e.g. mineral particles, plant debris, etc.), which show non-selective scattering, and
4. phytoplankton, which both scatter and absorb light, as dependent upon size, shape and type of pigments (Kirk 1975a,1975b,1976).

Crater Lake, Oregon is considered the most transparent fresh-water body on earth. The lake is consistently free of plankton and other organic material, and approaches distilled water in clarity and chemical content. A graph of its spectral sensitivity shows increasing absorption towards the long wave end of the spectrum and an exceptionally low K_{PAR} value of 0.037 ln units m^{-1} (Smith et al. 1973).

However, in most natural waters, light penetration is considerably less than that in Crater Lake. Furthermore, the light climate of a single lake is often highly variable, both diurnally and seasonally. On a single day, K_{PAR} varied by almost 2-fold in Long Loch and by almost 3-fold in Loch Drumore. Walmsley et al. (1980) reported a maximum 3-fold variation in K_{PAR} between nine sites in a subtropical reservoir, and attributed it to variability in turbidity caused by differing stratification and circulation patterns within the impoundment. Roemer and Hoagland (1979) observed K_{PAR} variations of 3-fold and 20-fold in two Nebraska reservoirs and concluded that the sites differed in turbidity as a result of proximity to inflow or the effect of frequent exposure to winds on sites of different depths.

In both Long Loch and Loch Drumore, neither K_R/K_{FR} nor ζ for a given depth exhibited variation between sites on a single day, although K_{PAR}, K_R, and K_{FR} were often highly variable. The attenuating component responsible for this variability must, therefore, be either non-selective over the entire PAR spectrum or selective only at the blue end of the spectrum. The latter possibility implicates gelbstoff, however no significant variability between sites was observed. Although the chlorophyll a concentration was significantly different between sites in both Long Loch and Loch Drumore, it can not be the causal agent as R light was not selectively attenuated. Furthermore, at the low phytoplankton concentrations reported here, light would be attenuated by predominantly non-algal material (Talling 1960b, Ganff 1974, Lorenzen 1980). Heterogeneous horizontal distribution of non-selective turbidity may account for the

regional variability in light attenuation.

Wind-induced turbidity may be responsible for the decreased light penetration towards the shore in Long Loch, the shallower water being more susceptible to the turbulent suspension of fine mineral and soil particles. In Loch Drumore, however, there is no constant relation in the variability between sites and, in this shallow lake, regional variation in light attenuation may relate to boating activities. Particulate matter, suspended in the narrow columns of open water by the passage of boats, may not be homogeneously distributed across the lake because of the restriction to turbulent flow imposed by the surrounding, dense Elodea canadensis beds. Localized 'ponds', delimited by blanketing vegetation, and showing different coefficients of light attenuation, could develop within the lake.

The seasonal variation in light penetration, as shown by K_{PAR}, is almost 3-fold in Long Loch (0.75 to 2.00 ln units m^{-1}) and almost 5-fold in Loch Drumore (0.60 to 2.80 ln units m^{-1}). In Lake Kinneret (Israel), Dubinsky and Berman (1979) measured K_{PAR} values of approximately 0.5 to 3.3 ln units m^{-1}. Spence et al. (1971a) reported a range in K_{PAR} of 1.30 to 2.90 ln units m^{-1} in eutrophic Loch Leven, while in a subtropical reservoir K_{PAR} varied from 0.64 to 2.99 ln units m^{-1} (Walmsley et al. 1980). In Australia, Kirk (1977) reported a seasonal range in K_{PAR} from Lake Burley Griffen of 1.91 to 5.04 ln units m^{-1}. The largest seasonal variation reported for a freshwater system occurred in McConaughy Reservoir, Nebraska, where K_{PAR} had a 34-fold range, from 0.37 to 12.54 ln units m^{-1} (Roemer and Hoagland 1979).

Seasonal variation in the penetration of light in many lakes has been attributed to changes in phytoplankton concentration (Talling 1965, Bindloss 1974, Ganff 1974, Jewson 1977, Dubinsky and Berman 1979, 1981). The seasonal variability in K_R/K_{FR} and ζ at a given depth suggest that in Long Loch and Loch Drumore varying phytoplankton concentrations are primarily responsible for seasonal fluctuations in light penetration. The strong, linear correlation (r=0.85) between chlorophyll *a* concentration and K_R (the minimum attenuation coefficient of the three spectral regions) confirms this relationship for Long Loch. The mean spectral attenuation coefficient of the algae (k_c) is 0.018 ln units mg^{-1} chlorophyll *a* m^{-2}, which falls within the range of 0.01 to 0.02 ln units mg^{-1} m^{-2} reported by Talling (1960b, 1970), Megard (1972), Bannister (1974), Ganff (1974), Jewson (1977), and Dubinsky and Berman (1979). The average background level of non-algal light attenuation in Long Loch has a k_w value of 0.68 ln units m^{-1}, which is similar to the value of 0.74 ln units m^{-1} reported by Bindloss (1974) for Loch Leven and the 0.69 ln units m^{-1} reported by Dubinsky and Berman (1979) for Lake Kinneret (Israel). Lorenzen (1980) suggests that a background light attenuation value of 0.05 ln units m^{-1} represents the limit for the clearest waters.

The influence of background light attenuation is most apparent at low chlorophyll *a* concentrations. From the regression equation of chlorophyll *a* concentration (C) on K_R:

$$K_R = k_c C + k_w$$

the fraction (F) of total subsurface light attenuated by chlorophyll can be calculated (Bannister 1974):

$$F = k_c C \; / \; k_c C + k_w$$

which is equivalent to (Megard et al. 1980):

$$F = C \; / \; C + (k_w/k_c).$$

Thus, when k_w/k_c equals C the phytoplankton attenuate fifty percent of the subsurface light, whereas when k_w/k_c is greater than C, the background attenuation exceeds the attenuation by chlorophyll. It is only when C becomes much greater than k_w/k_c that the effect of k_w becomes insignificant.

Using the regression equation for Long Loch, $K_R=0.018C + 0.68$, the percentage light attenuation due to the algae at various K_R values can be determined, as illustrated in Fig. 4.12. At chlorophyll concentrations less than 34µg l^{-1} (i.e. $K_R<1.3$), more than half of the light attenuation is due to non-algal material, while at the most frequently observed chlorophyll a concentration, 10µg l^{-1}, approximately eighty percent of the subsurface light attenuation is due to material other than chlorophyll a. Thus, the scatter observed in Fig. 4.7 at low chlorophyll concentrations may arise from day-to-day variation in background light attenuation. At higher phytoplankton concentrations the scatter may be attributed to variation in k_c due to the physiological state (Dubinsky and Polna 1976), geometry and cell size (Kirk 1975a, 1975b, 1976) of the component algal species.

In Loch Drumore, the observed chlorophyll a concentrations were usually less than 30µg l^{-1} and, in relation to K_R, showed a random distribution. At these low concentrations, subsurface light is predominantly attenuated by non-algal material and the relationship

between phytoplankton concentration and light attenuation can not be discerned.

It is very difficult to draw any conclusions from field data regarding the possible role of light quantity and quality on turion production in P. crispus and P. obtusifolius. The complex interactions between algae, turbidity, gelbstoff, and the attenuation of incident light are difficult to assess and quantify. Furthermore, a comprehensive picture of underwater light quantity, with particular respect to PAR, can only be attained by combining seasonal K_{PAR} measurements with integrated measurements of incident irradiance. Nonetheless, the considerable variation in light attenuation within a single lake at any one time, let alone between lakes, suggests that neither seasonal variation in light quantity nor light quality is likely to represent the primary environmental cue triggering turion production. The field observations show that turion production is associated with high temperatures and long days in P. crispus and with high temperatures and decreasing photoperiods in P. obtusifolius, thus suggesting that dormancy induction may be environmentally controlled by temperature and photoperiod. However, in order to assess the role of photoperiod, temperature and, in particular, light quantity and quality on turion production, controlled laboratory experiments are essential.

Fig. 4.1. Seasonal variation in the vertical diffuse attenuation coefficients (K $\pm$ S.E.) for PAR, R, and FR light (ln units m^{-1}) within each of three depth classes in Long Loch ($\triangle$, less than 2.5m; $\bullet$, between 2.5 and 4.5m, inclusive; $\square$, greater than 4.5m). Turion production by *P. crispus* is indicated by (⊢——⊣).

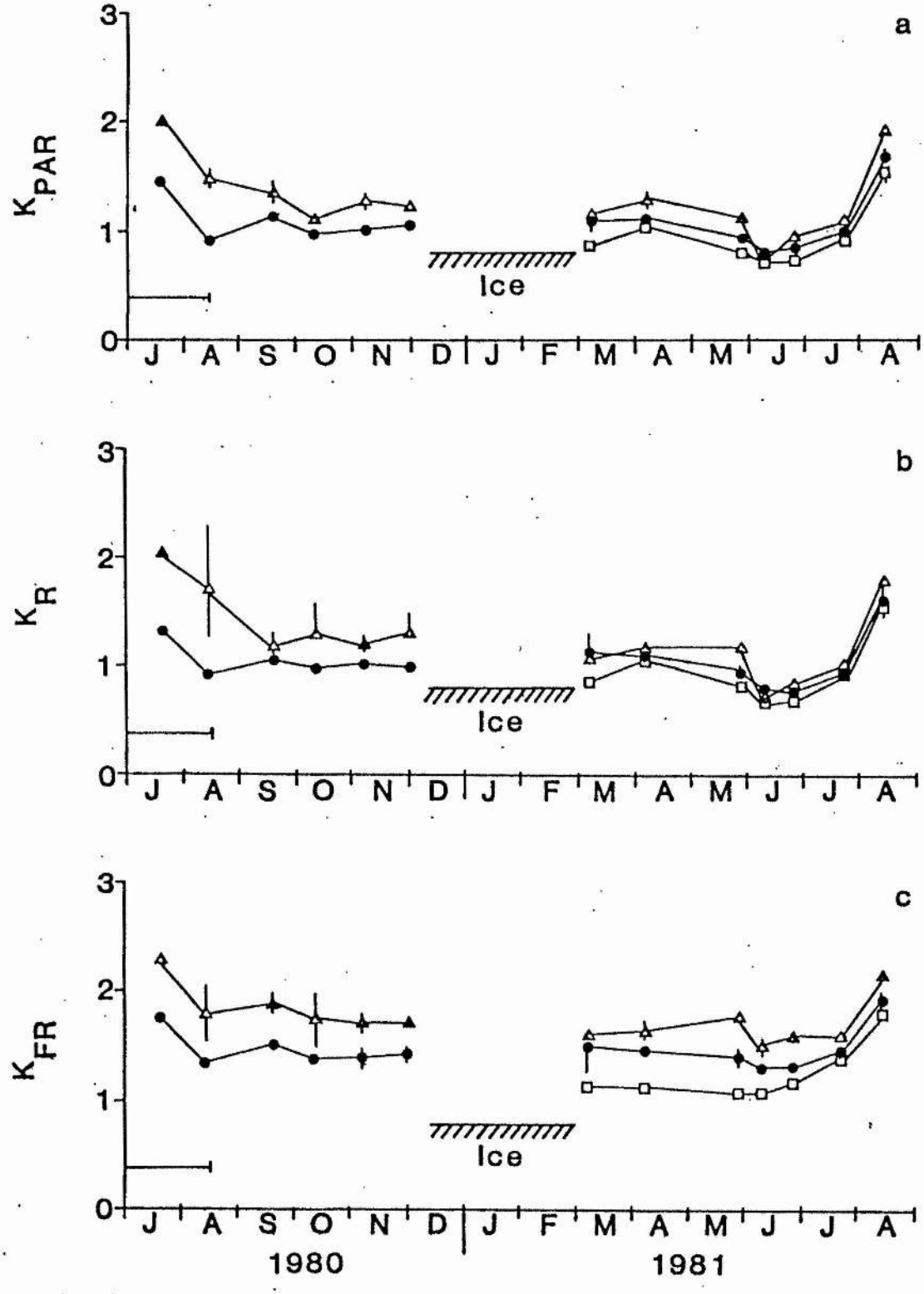

a
b
c
K_{PAR}
K_R
K_{FR}
3
2
1
0
Ice
J A S O N D J F M A M J J A
1980
1981

Fig. 4.2. Seasonal variation in the ratio of K_R to K_{FR} ($K_R/K_{FR} \pm$ S.E.) and ζ ($\pm$ S.E.) for all depth classes in Long Loch. Turion production by P. crispus is indicated by (⊢——⊣).

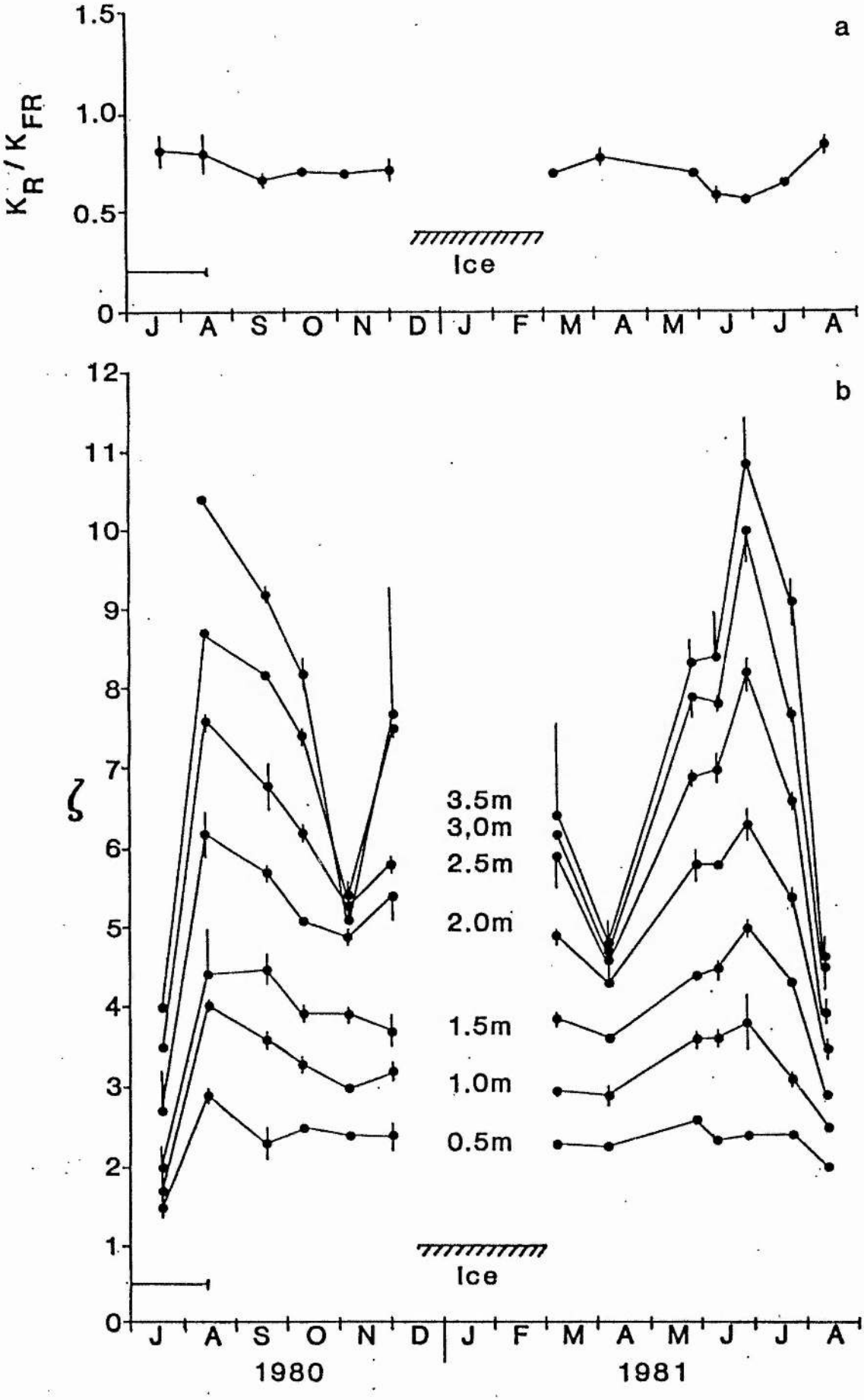

a
K_R / K_{FR}
1.5
1.0
0.5
0
Ice
J A S O N D J F M A M J J A
b
ζ
12
11
10
9
8
7
6
5
4
3
2
1
0
3.5m
3,0m
2.5m
2.0m
1.5m
1.0m
0.5m
Ice
J A S O N D J F M A M J J A
1980
1981

Fig. 4.3. Seasonal variation in the vertical diffuse attenuation coefficients (K $\pm$ S.E.) for PAR, R, and FR light (ln units m^{-1}) at site 1, $\triangle$, site 2, $\bullet$, and site 3, $\circ$, in Loch Drumore. Turion production by P. crispus and P. obtusifolius is indicated by (⊢——⊣) and (⊢------⊣), respectively.

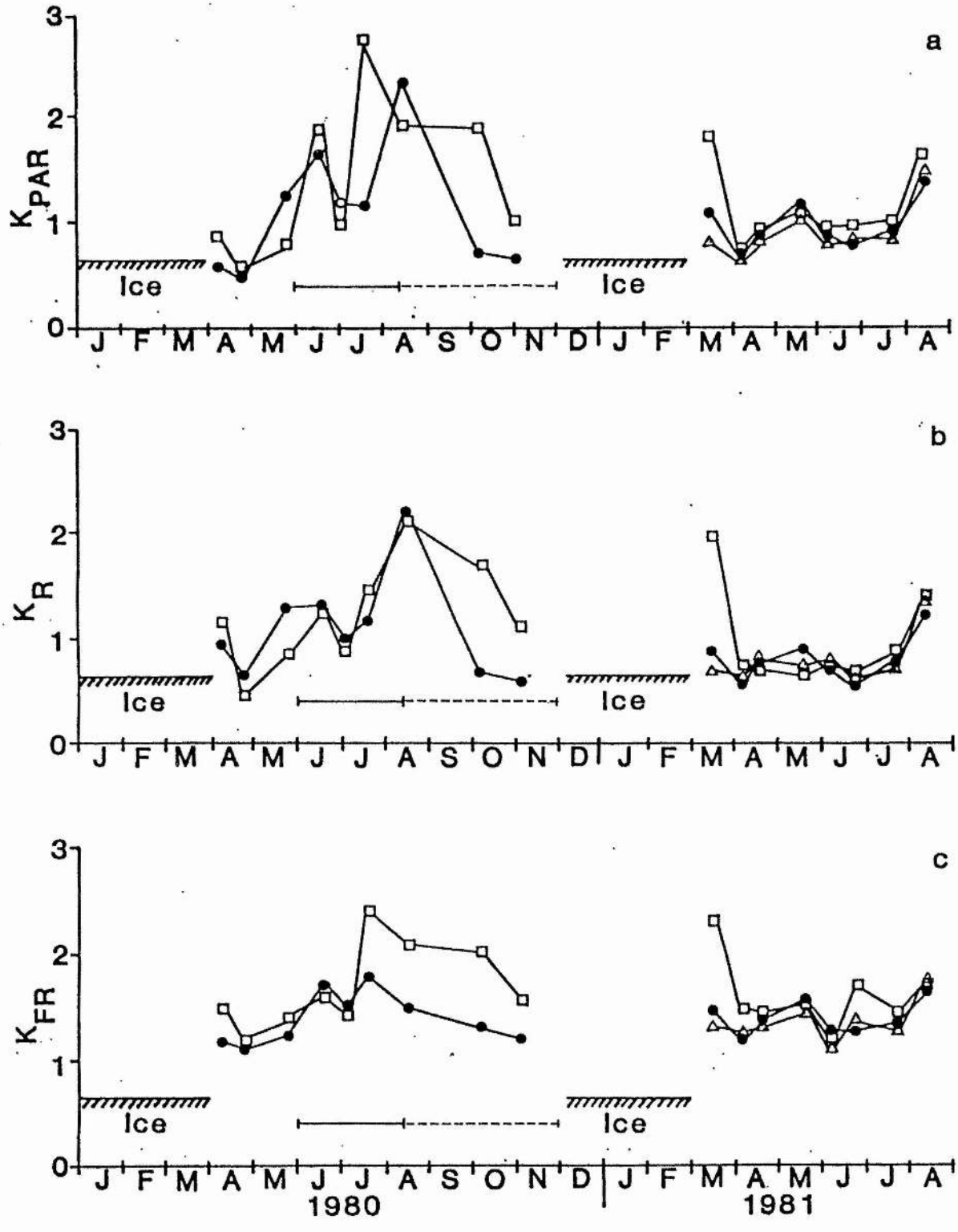

a
b
c
K_{PAR}
K_R
K_{FR}
0
1
2
3
Ice
Ice
J F M A M J J A S O N D J F M A M J J A
1980
1981

Fig. 4.4. Seasonal variation in the ratio of K_R to K_{FR} ($K_R/K_{FR} \pm$ S.E.) and ζ ($\pm$ S.E.) for all marked sites in Loch Drumore. Turion production by P. crispus and P. obtusifolius is indicated by (⊢——⊣) and (⊢-----⊣), respectively.

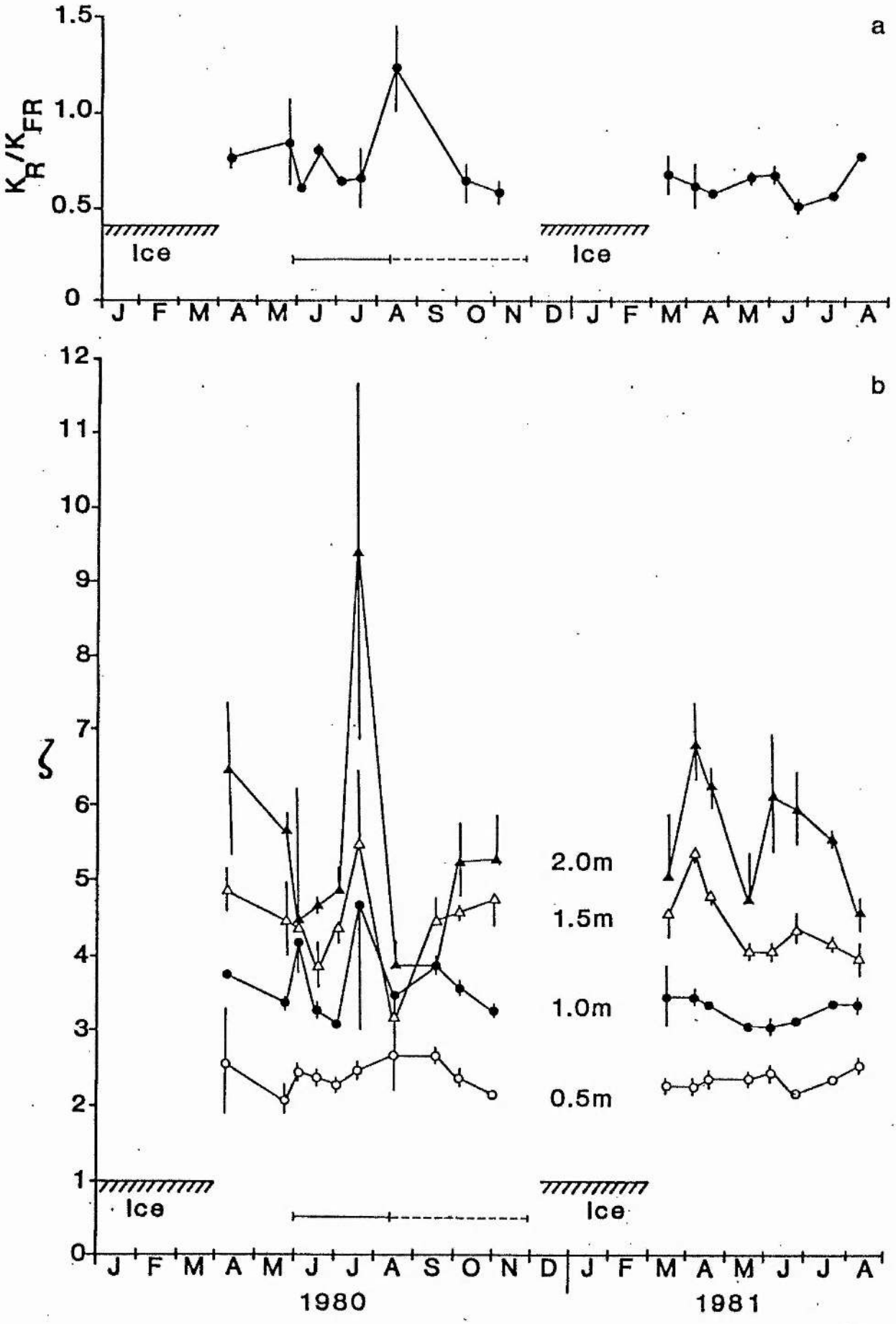

a
K_R/K_{FR}
1.5
1.0
0.5
0
Ice
Ice
J F M A M J J A S O N D J F M A M J J A
b
ζ
12
11
10
9
8
7
6
5
4
3
2
1
0
2.0m
1.5m
1.0m
0.5m
Ice
Ice
J F M A M J J A S O N D J F M A M J J A
1980
1981

Fig. 4.5. Seasonal variation in the vertical diffuse attenuation coefficients for PAR, R, and FR light at two or three unmarked sites in a P. praelongus/E. canadensis bed in Loch Drumore. Each point represents the K value (ln units m^{-1}) for an individual site and vertical lines connect attenuation coefficients measured on the same day.

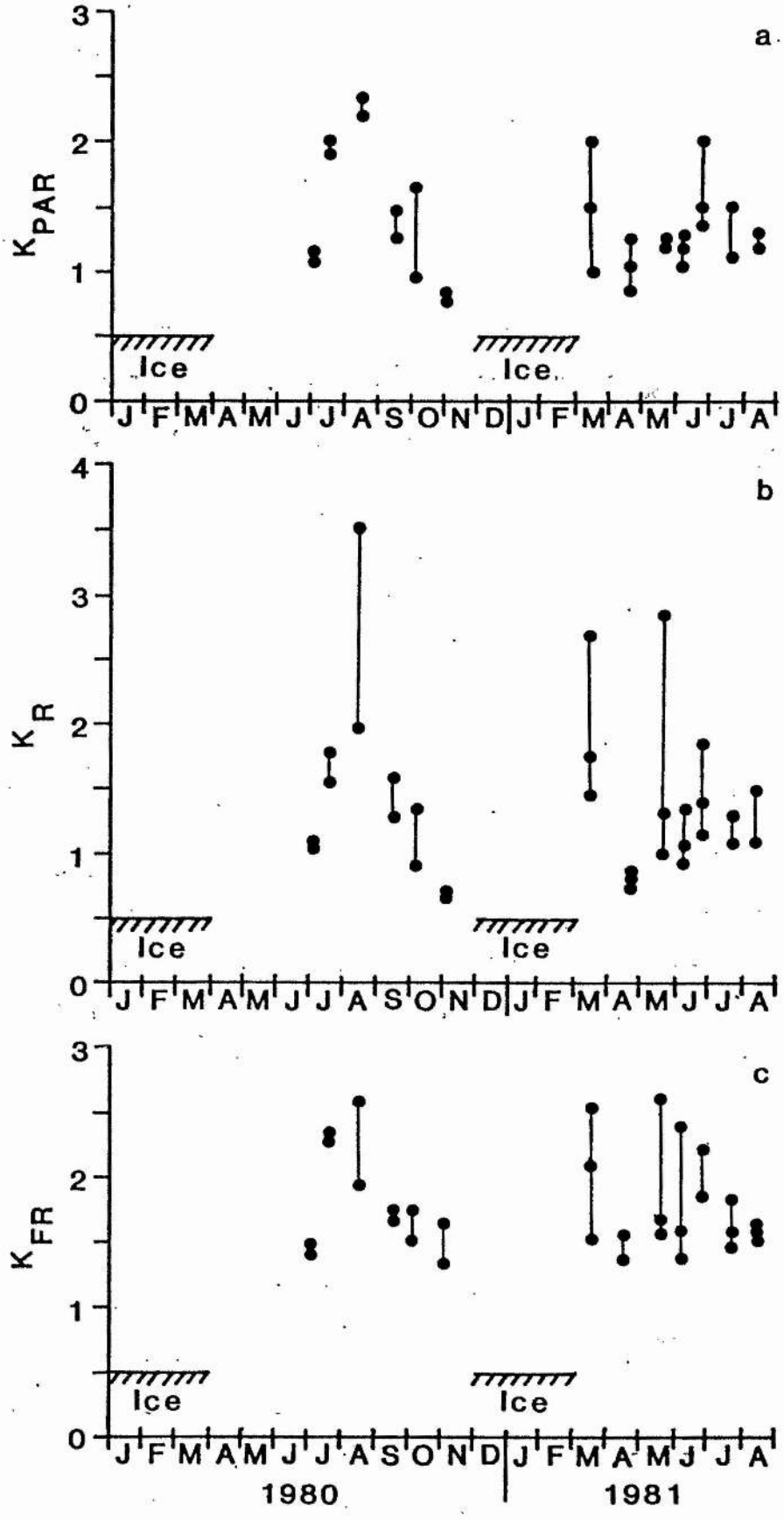

a
b
c
K_{PAR}
K_R
K_{FR}
Ice
Ice
Ice
Ice
Ice
Ice
J F M A M J J A S O N D J F M A M J J A
1980
1981

Fig. 4.6. Seasonal variation in gelbstoff concentration (expressed as absorbance), chlorophyll *a* concentration, ζ , and the vertical diffuse attenuation coefficients (K_{PAR}, K_R, K_{FR}, and K_R/K_{FR}) for sites greater than 4.5m deep in Long Loch.

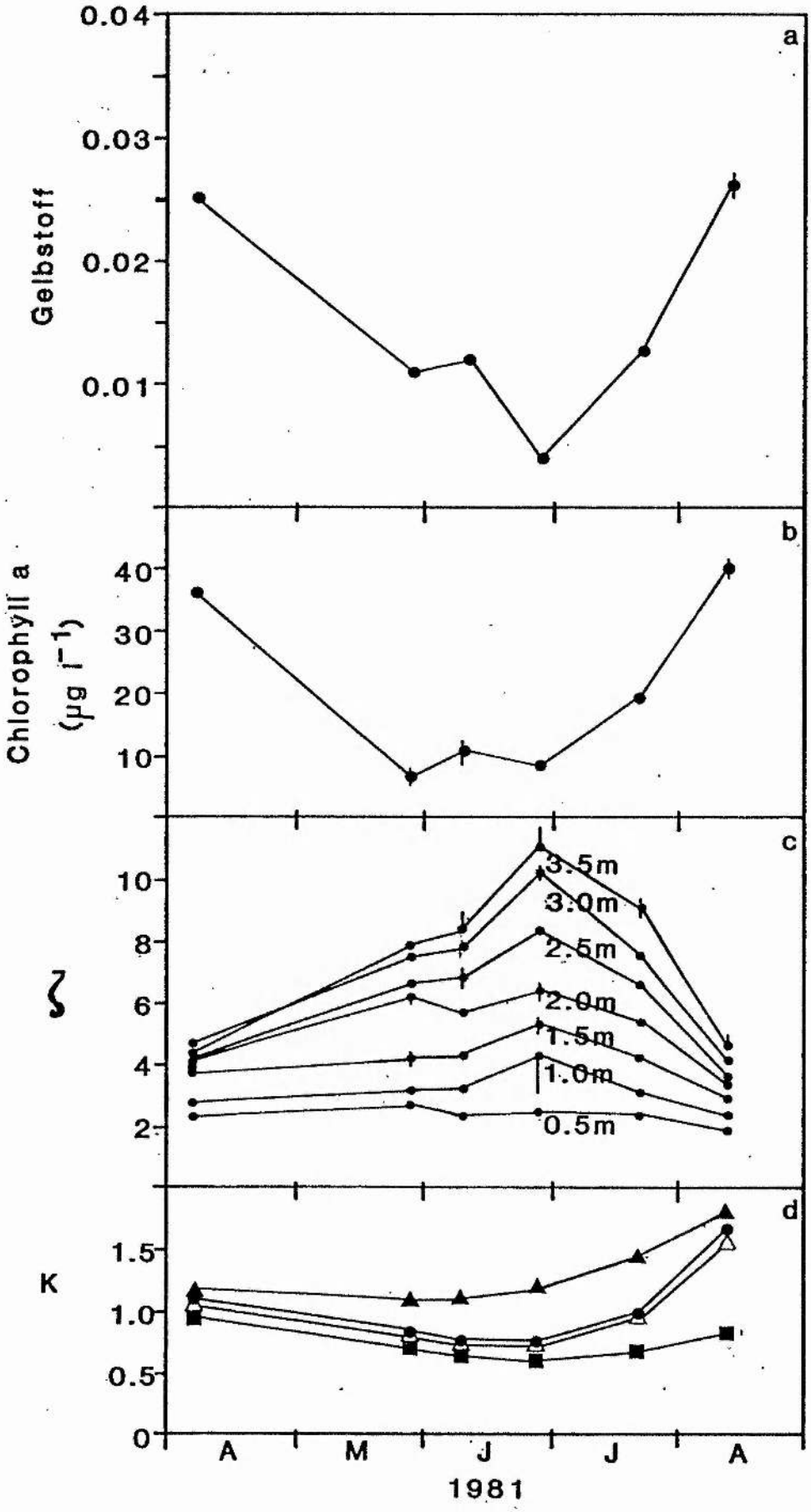

a
Gelbstoff
0.04
0.03
0.02
0.01
b
Chlorophyll a
(µg l⁻¹)
40
30
20
10
c
ζ
10
8
6
4
2
3.5m
3.0m
2.5m
2.0m
1.5m
1.0m
0.5m
d
K
1.5
1.0
0.5
0
A
M
J
J
A
1981

Fig. 4.7. Seasonal variation in the vertical diffuse attenuation coefficient for R light in relation to chlorophyll a concentration in Long Loch.

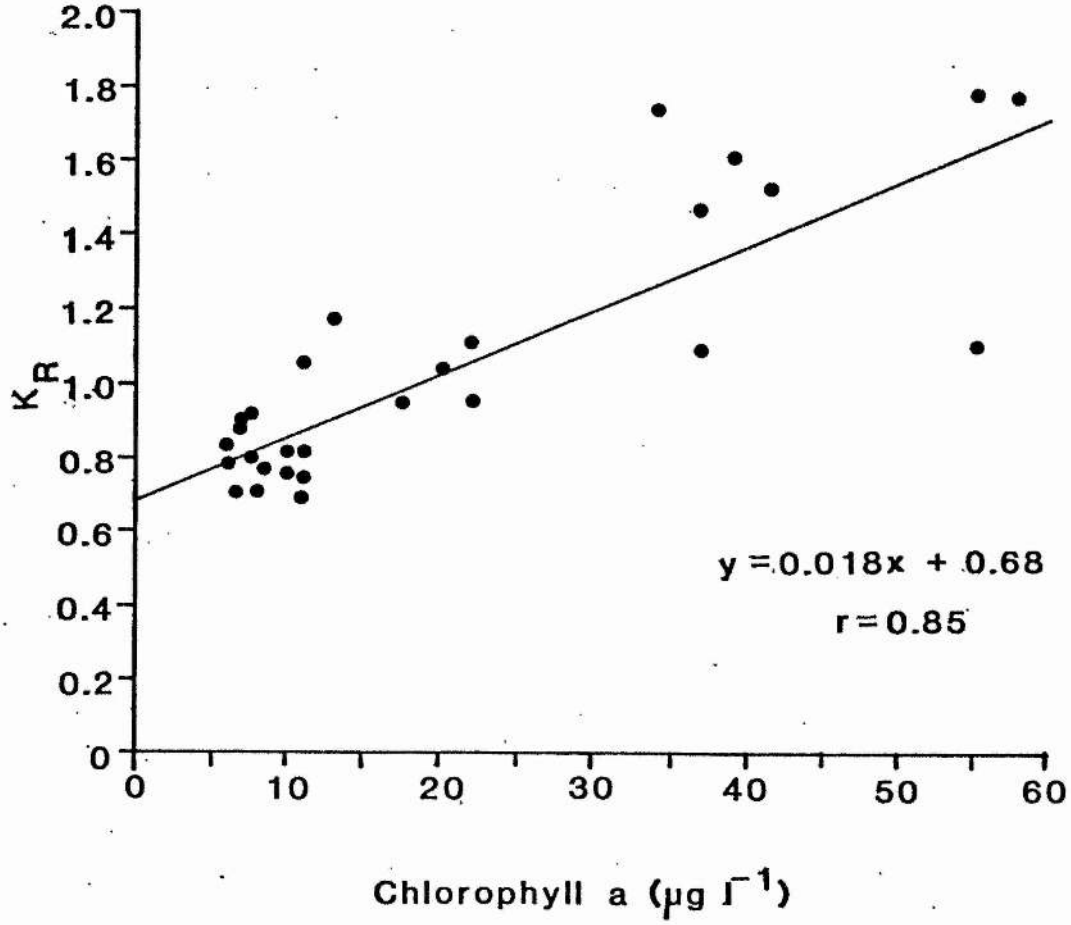

2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
K_R
0
10
20
30
40
50
60
y = 0.018x + 0.68
r = 0.85
Chlorophyll a (µg l^{-1})

Fig. 4.8. Seasonal variation in gelbstoff concentration (expressed as absorbance), chlorophyll a concentration, ζ, and the vertical diffuse attenuation coefficients (K_{PAR}, K_R, K_{FR}, and K_R/K_{FR}) at site 1 (open water) in Loch Drumore.

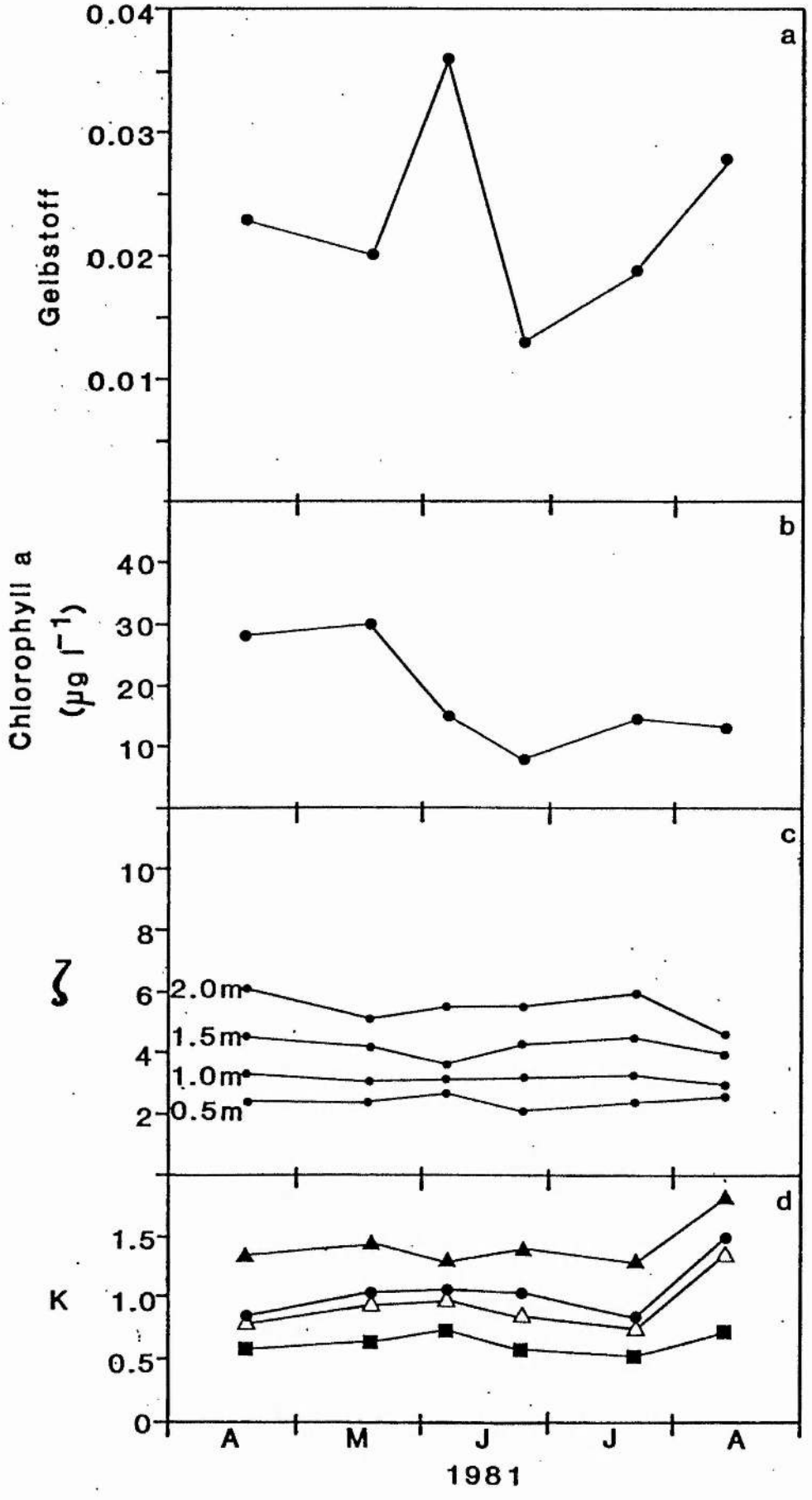

a
Gelbstoff
0.04
0.03
0.02
0.01
b
Chlorophyll a
(µg l⁻¹)
40
30
20
10
c
ζ
10
8
6
4
2
2.0m
1.5m
1.0m
0.5m
d
K
1.5
1.0
0.5
0
A
M
J
J
A
1981

Fig. 4.9. Seasonal variation in the vertical diffuse attenuation coefficient for R light in relation to chlorophyll a concentration in Loch Drumore.

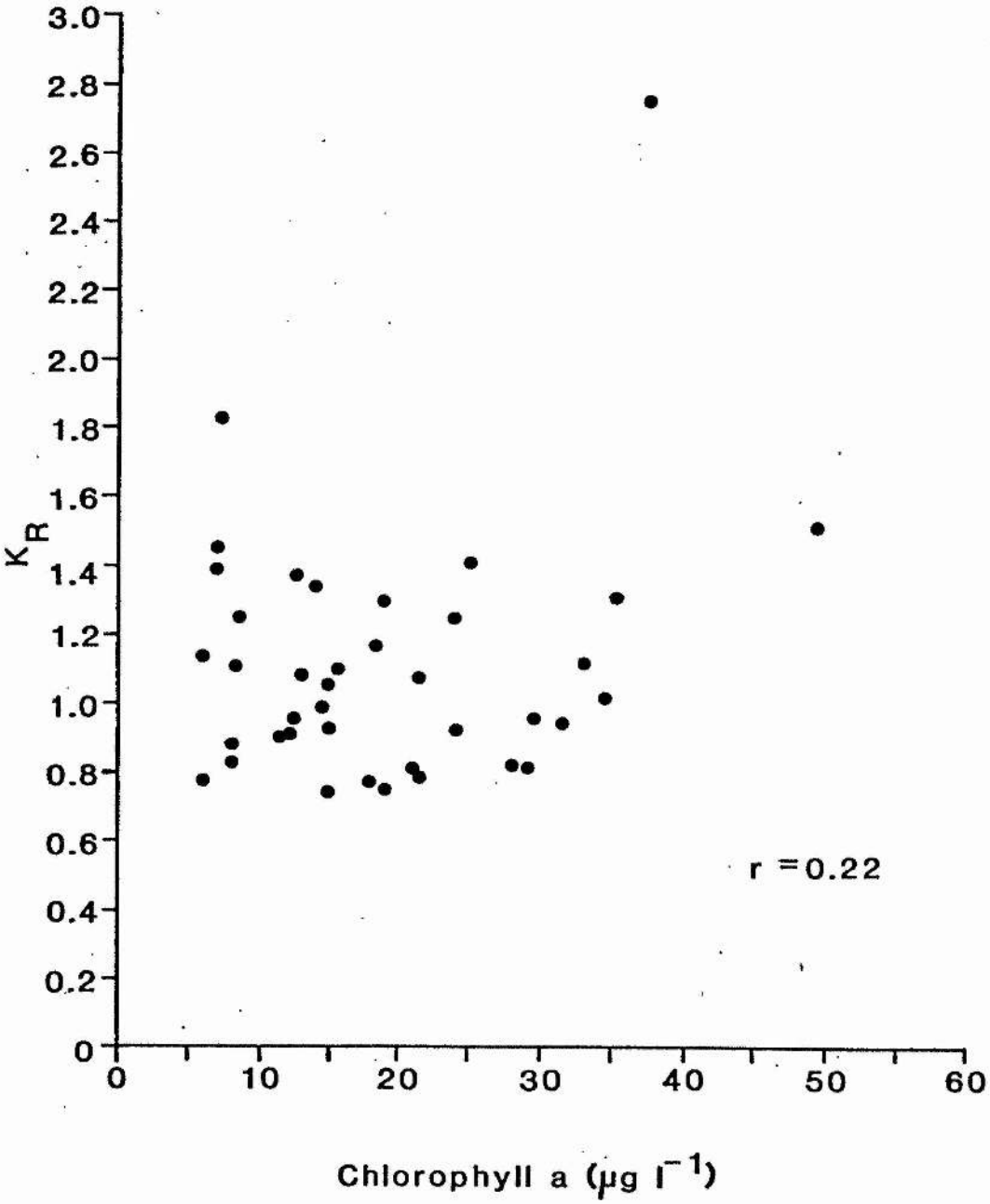

3.0
2.8
2.6
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
K_R
0
10
20
30
40
50
60
r =0.22
Chlorophyll a (µg l^{-1})

Fig. 4.10. Seasonal variation in temperature, (———), and photoperiod, (------), for Long Loch. The photoperiodic data were obtained from the Nautical Almanac and Astronomical Ephemeris (1944). Turion production by P. crispus is indicated by (⊢———⊣).

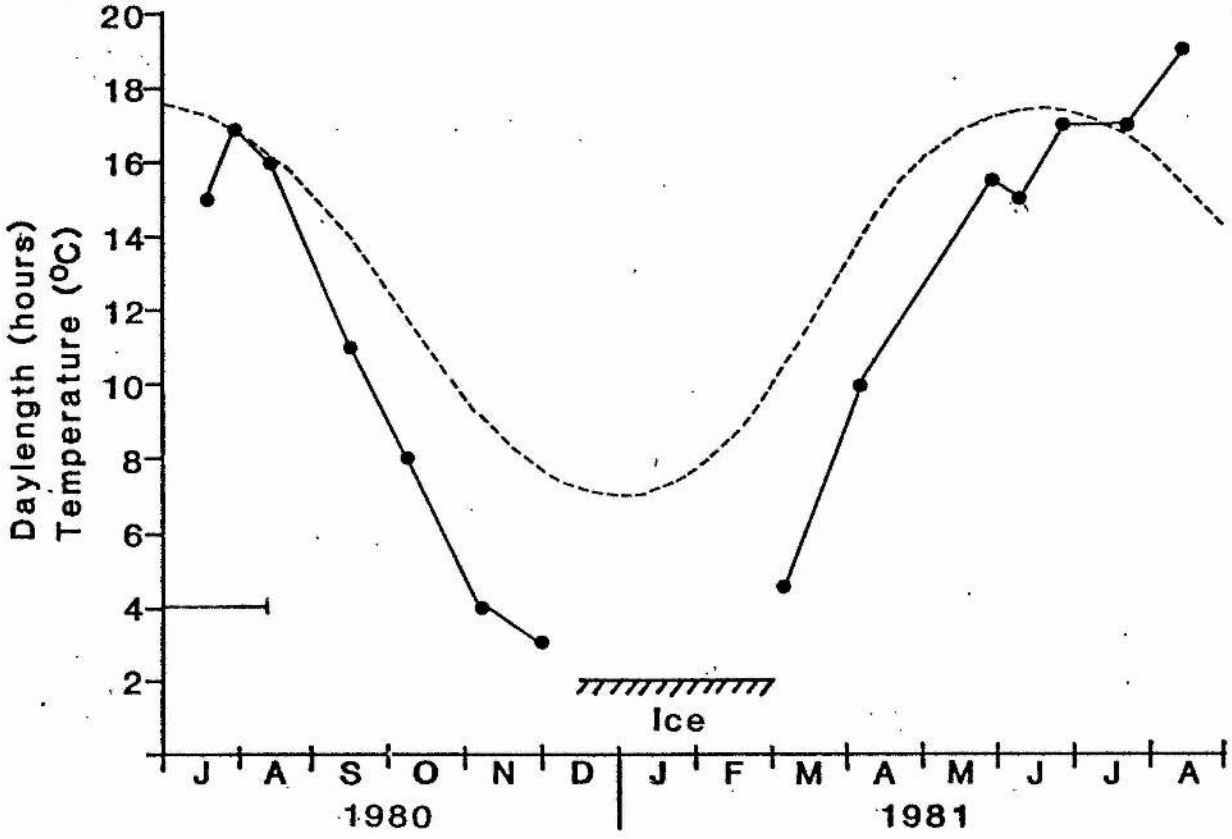

Daylength (hours)
Temperature (°C)
20
18
16
14
12
10
8
6
4
2
Ice
J
A
S
O
N
D
J
F
M
A
M
J
J
A
1980
1981

Fig. 4.11. Seasonal variation in temperature, (———), and photoperiod, (-------), for Loch Drumore. The photoperiodic data were obtained from the Nautical Almanac and Astronomical Ephemeris (1944). Turion production is P. crispus and P.obtusifolius is indicated by (⊢———⊣) and (⊢-----⊣), respectively.

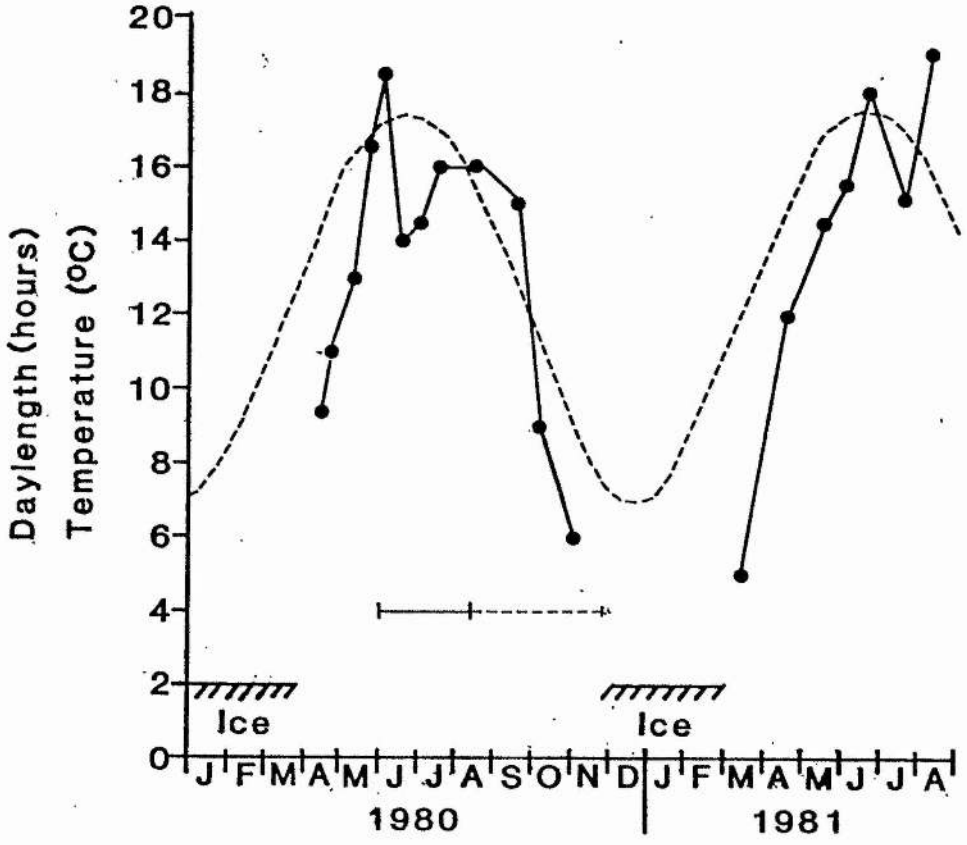
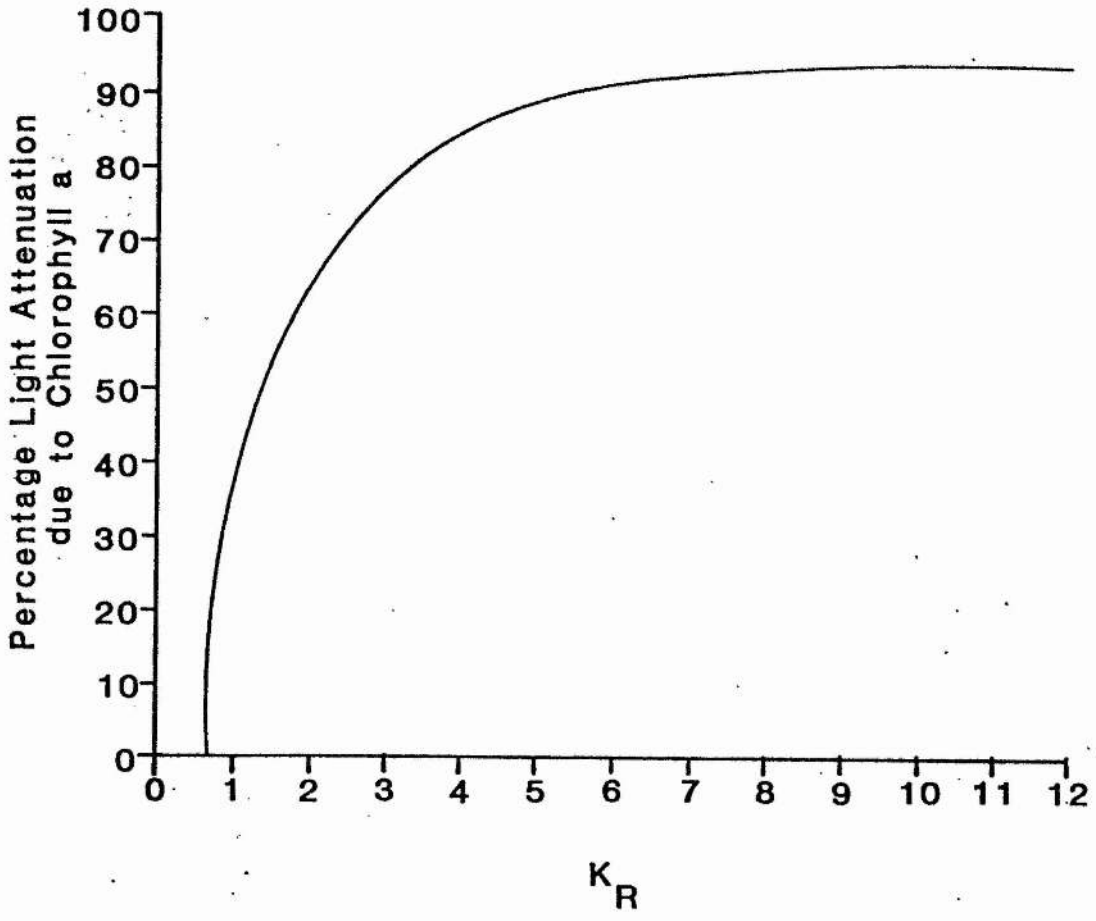

Daylength (hours)
Temperature (°C)
20
18
16
14
12
10
8
6
4
2
0
Ice
Ice
J F M A M J J A S O N D J F M A M J J A
1980
1981

Fig. 4.12. Percentage of total R light attenuated in Long Loch which can be attributed to chlorophyll *a* ($\mu g\ mg^{-2}$) over a range of K_R values.


Percentage Light Attenuation due to Chlorophyll a
100
90
80
70
60
50
40
30
20
10
0
0 1 2 3 4 5 6 7 8 9 10 11 12
K_R

CHAPTER 5

DIURNAL VARIATION IN THE AQUATIC LIGHT CLIMATE

5.1 INTRODUCTION

In order to accurately determine time of year, the time-measuring mechanism in photoperiodically sensitive plants must operate with a high degree of precision and must also be relatively insensitive to random variations in the environment. It was originally assumed that daylength was perceived by dawn and dusk changes in the PAR photon fluence rate. However, diurnal fluctuations in cloud cover could seriously disrupt the photoperiodic clock. The recent observations on diurnal variation in the R and FR spectral energy distribution of natural daylight revealed that twilight is characterized by a distinct decrease in ζ from the midday value (Robertson 1966, Scott et al. 1968, Evans 1969, Sinclair and Lemon 1973, Monteith 1976, Holmes and McCartney 1976, Holmes and Smith 1977a). Consequently, Vince-Prue (1975, 1976) proposed that phytochrome monitors the quality of the incident light and acts as a regulator of photoperiodic timing for terrestrial plants (Vince-Prue 1975, 1976). The onset of twilight, as determined by a reduction in ζ, is dependent only upon astronomical time and thus, ζ may function as a reliable signal for measuring daylength.

Many photoperiodic effects have been reported for aquatic plants, including flowering, (Krajncic and Devide 1980), turion germination (Weber and Nooden 1976a), and turion production (Heslop-Harrision 1962, Weber and Nooden 1974, Winston and Gorham 1979). The objective of the present study was to investigate the diurnal variation in the attenuation of underwater light, with particular emphasis on the R and FR wavelength bands, in order to determine whether ζ could act as a photoperiodic clock for aquatic plants.

5.2 RESULTS

Figures 5.1, 5.2, and 5.3 illustrate the diurnal changes in ζ and the attenuation of PAR and the R and FR wavelength bands in Loch Lomond, Loch Drumore, and Fingask Loch, respectively. The attenuation of R to FR light (K_R/K_{FR}) remained relatively constant throughout the midday in each of the three lochs. However, a marked increase in underwater ζ was observed at dawn. At dusk, a complimentary decrease in ζ from the midday values was observed, however the minimal dawn values were never attained.

In Loch Lomond, the twilight changes in ζ, particularly at dusk, were usually proportional with depth and corresponded to the changes in incident ζ. At dawn, a trend was indicated towards a reduction in ζ at depths greater than 2.5m, however the photon fluence rates were too low to obtain accurate measurements. K_R and K_{FR} remained constant

throughout the day until the descent of the sun below the hills at 18.30 GMT, when there was a significant increase in K_R ($p<0.05$), K_{FR} ($p<0.01$), and K_R/K_{FR} ($p<0.05$).

In Loch Drumore, the increase in ζ at dawn was not proportional with depth, as ζ approached equality for all depths at first light. A highly significant increase ($p<0.01$) in K_{FR} and a slight decrease ($p<0.05$) in K_R, resulted in an increase ($p<0.05$) in K_R/K_{FR} during early morning and established the midday pattern of increasing ζ with depth. At dusk, the decrease in ζ was proportional with depth and there was no significant change ($p>0.05$) in the light attenuation coefficients.

The twilight changes in spectral light quality were most dramatic in Fingask Loch, where ζ rapidly decreased with increasing depth. At dawn, K_{FR} increased ($p<0.01$) from 0.78 ln units m^{-1} at first light to 1.39 ln units m^{-1} two hours later. Concurrently, a significant reduction ($p<0.01$) in K_R from 2.03 ln units m^{-1} to 1.59 ln units m^{-1} was observed. These changes resulted in a two-fold decrease in K_R/K_{FR} (from 2.63 to 1.16 ln units m^{-1}) at dawn ($p<0.01$). At dusk, there was a complimentary, but reverse, shift in attenuation of the R and FR wavelength bands. An increase ($p<0.01$) in K_R and a decrease ($p<0.01$) in K_{FR} resulted in an increase in K_R/K_{FR} ($p<0.01$) at dusk. However, the magnitude of this shift was much smaller than that observed at dawn.

At midday ζ for a given depth was markedly different between the three lochs. At a depth of 2.5m, ζ was 9.03 in Loch Lomond, 8.83 in Loch Drumore, and 2.44 in Fingask Loch. The reduction in ζ at a given depth over the three lochs corresponded to increasing chlorophyll a concentrations of 3.0µg l^{-1} in Loch Lomond, 19µg l^{-1} in Loch Drumore, and 40µg l^{-1} in Fingask Loch.

5.3 DISCUSSION

The radiation reaching the earth's surface during the day is composed of both direct solar radiation, which is rich in R and FR light, and scattered skylight, which is rich in blue light. The spectral energy distribution of direct radiation is dependent upon optical air mass. Increasing air mass (i.e. decreasing solar elevation) results in selective attenuation of the shorter wavelengths due to the increased path length through the ozone layer, which absorbs broadly around 600nm (McFarland 1975). The spectral energy distribution of scattered radiation is dependent upon angular distance from the sun, solar elevation, and atmospheric transmissivity (Hess 1939 and Linke 1942 cited in Holmes and Smith 1977a).

Throughout the daylight hours, the spectral energy distribution in the range 300 to 800nm remains relatively constant and is independent of cloud cover, although the PAR photon fluence rates on clear and overcast days are very different (Hull 1954, Robertson 1966,

Federer and Tanner 1966, Scott et al. 1968, Kondratjev 1969, Sinclair and Lemon 1973, Holmes and McCartney 1976). At midday, ζ as incident upon both Loch Lomond and Fingask Loch, was approximately 1.5, which is slightly larger than the mean values of 1.14 and 1.15 reported by Sinclair and Lemon (1973) and Holmes and Smith (1977a), respectively.

At twilight, there was a drop in ζ (to approximately 1.2 above both lochs), attributable to an increase in scattered radiation and a decrease in direct radiation. Prior to sunrise, there is an increase in energy at the blue end of the spectrum; this is followed by an increase in R and an even greater increase in FR light, resulting in a decrease in ζ (Robertson 1966, Holmes and McCartney 1976). As the solar angle increases, the R contribution increases more rapidly than the FR, thus increasing ζ to the equilibrium level maintained throughout the day.

At sunset the reverse sequence occurs, such that during early twilight there is an increase in energy at the blue and R ends of the spectrum with a concomitant decrease in ζ. During late twilight (approximately 30 minutes after sunset) there is a shift in the spectral energy distribution almost entirely towards the blue (McFarland 1975, Holmes and McCartney 1976, Holmes and Smith 1977a).

Holmes and Smith (1977a) reported twilight values of ζ which ranged from 14 to 44 percent lower than the midday value, the rate, magnitude, and duration of ζ shifts being dependent upon atmospheric conditions. Totally overcast skies produced the smallest and most gradual shifts whereas the largest and most erratic shifts occurred

under clear or partially clear skies (Holmes and McCartney 1976, Holmes and Smith 1977a). Under overcast conditions a shift in incident ζ of approximately 15 to 20 percent was observed for both Loch Lomond and Fingask Loch.

Underwater twilight shifts in ζ were usually of much larger magnitude than those observed above the lake surface. The attenuation of radiation for a specific wave-length in distilled water is expressed by the Beer-Lambert law:

$$I = I_o \cdot e^{Kz},$$

equivalent to:

$$K = \frac{\ln I_o - \ln I_z}{z}$$

where K is the attenuation coefficient, I_o is the PAR photon fluence rate at the surface, and I_z is the PAR photon fluence rate at depth z. The attenuation coefficient, K, is equal to the sum of the mean spectral attenuation coefficient of the algae, k_c, and the attenuation coefficient of water and non-chlorophyll, light-attenuating compounds, k_w. In distilled water K is equal to k_w, the attenuation coefficient of water. As water selectively attenuates light of longer wavelengths, there is a logarithmic decrease in R light and an even greater rate of logarithmic decrease in FR light with depth. Thus, in distilled water, ζ will increase linearly with depth and the value of ζ at any given depth will be determined by the value of the incident ζ. The decrease in incident ζ at twilight would, therefore, cause a proportional decrease in ζ at each depth; K_R and K_{FR} would remain constant.

However, in natural waters K is equal to the sum of k_c and k_w. Thus, where k_c is large in comparison with k_w, ζ does not increase linearly with depth. The value of ζ at any given depth is determined not only by the incident ζ, but also by the biomass of algae in the water. Figure 5.4 illustrates the relationship between mean ζ (from Figures 5.1, 5.2, and 5.3) and chlorophyll a biomass (the product of chlorophyll a concentration and depth, expressed as mg m^{-2})with depth for Loch Lomond, Loch Drumore, and Fingask Loch at both dawn and midday. Within each lake there is a linear relationship between ζ and algal biomass, the slope and direction of which is determined by chlorophyll a concentration. Loch Lomond, with the lowest chlorophyll a concentration (3µg l^{-1}), has the greatest increment in ζ per unit increase of algal biomass (termed ζ_c) and Fingask Loch, with the highest chlorophyll a concentration (40µg l^{-1}), has the smallest ζ_c. The isobaths, which connect points of equal depth, show a linear relationship between ζ and chlorophyll a biomass, the strength of the correlation being primarily dependent upon the similarity in k_w between the three lochs.

The shift from dawn to midday in the aquatic light climate is characterized by two changes:

1. a proportional increase in ζ at zero chlorophyll (i.e. an increase in the y-intercept) for each isobath, the slope of each isobath remaining relatively constant, and
2. an increase in ζ_c for each lake.

The midday increase in the isobath ordinate intercepts is caused by the shift in incident ζ from a low value at dawn (about 1.2) to an approximately 20 percent higher value at midday (about 1.5). As the ordinate represents zero chlorophyll (at an undetermined k_w), the proportional increase in ζ with depth at midday corresponds to the theory for distilled water. The slope of each isobath remains relatively constant between dawn and midday (given the variability which arises from unequal k_w values for the three lochs and the limited data set) and thus, at midday, the relationship between ζ and biomass is proportionately larger.

Figure 5.5 illustrates the relationship between ζ and biomass in a wheat crop (Triticum aestivum) at low and high solar angles, corresponding to dawn and midday, as calculated from Figures 1 and 7 of Holmes and Smith (1977b). Increase in biomass in the wheat crop with depth was approximately logarithmic. The relationship between ζ and biomass in the wheat crop increased proportionately with increasing solar angle, analogous to that found in aquatic systems.

However, in the underwater environment, midday ζ values are further augmented by an increase in the increment in ζ per unit increase of algal biomass (ζ_c). The midday increase in ζ_c correlates to changes in K_R and K_{FR}. In Loch Drumore, there was a decrease in K_{FR}, while in Fingask Loch K_{FR} decreased and K_R increased at dawn. Loch Lomond showed no significant change ($p > 0.05$) in K_R and K_{FR} from dawn to midday, which corresponds to a very small ζ_c shift. However, the midday increase in ζ_c between the three lochs does not

directly relate to increasing chlorophyll a concentrations, although the smallest change in ζ_c occurred at the lowest chlorophyll a concentration, viz Loch Lomond.

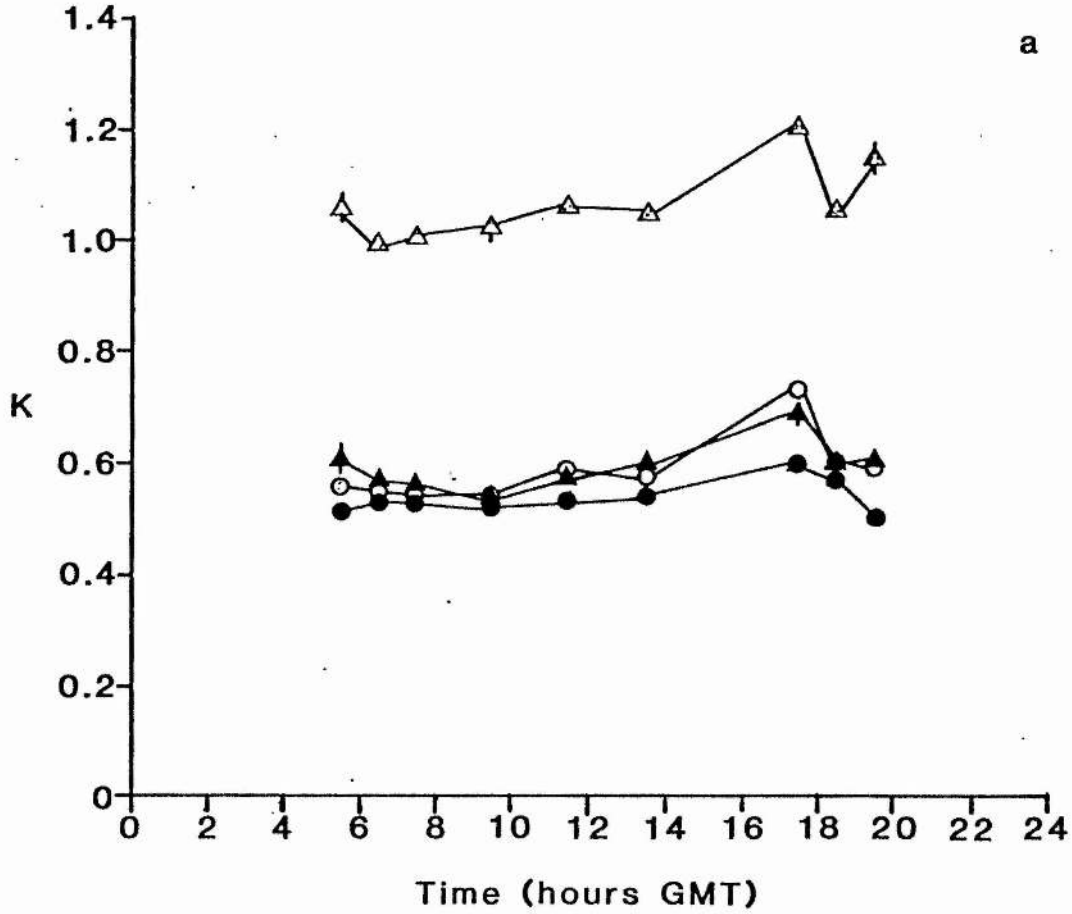
The high correlation coefficients ($r > 0.94$) from the determinations of K (the linear regression of the natural logarithms of the photon fluence rate on depth) confirm that the water columns in all three lochs were optically homogeneous. Thus, the shifts in ζ_c cannot be attributed to a gradual influx of selectively attenuating material. Diurnal variation in selective attenuation must, therefore, be exhibited by material, either physical or biological, present in the profiles throughout the day. Differential spectral attenuation by physical matter in the profiles could only result from changes in orientation. However, all measurements of light penetration were conducted in the euphotic zone, which is characterized by circulating water; physical particles are assumed to be randomly orientated.

Differential attenuation by algae may be attributed to variation in geometry and cell size (Kirk 1975a, 1975b, 1976), pigmentation, (Dubinsky and Polna 1976), or orientation. Regular changes in shape of phytoplankton are unlikely to occur daily, nor are pigmentation changes relating to senescence. Phytochrome exhibits daily variation in its spectral absorption properties as determined by incident ζ (Smith and Holmes 1977), however the small quantity of phytochrome present in plant cells could not account for the large ζ_c shifts observed here (B. Frankland, pers. comm.). Motile phytoplankton and zooplankton may exhibit daily variation in spectral attenuation due to changes in orientation (i.e. mode of presentation to the sun). In

Long Loch and Loch Drumore the twilight ζ shifts are caused, primarily, by changes in K_{FR}. Most biological organisms do not absorb, but instead scatter, light of 730nm. Daily changes in ζ_c may result from differential scattering of FR light by motile organisms. In order to test this hypothesis, independent diurnal measurements of absorption and scattering in clear and planktonic lakes are needed.

The data presented here show that the underwater spectral energy distribution of natural light exhibits predictable diurnal variation. Twilight is characterized by a decrease in ζ, proportional to or greater than that observed in terrestrial systems. Therefore, the concomitant shift in phytochrome photoequilibrium may, as hypothesized for terrestrial plants, function as a photoperiodic clock for aquatic macrophytes.

Fig. 5.1. Diurnal change in the vertical diffuse attenuation coefficients (K_{PAR}, ▲, K_R, O, K_{FR}, △, K_R/K_{FR}, ●, ± S.E.) and ζ (± S.E.) in Loch Lomond on 25 August 1981. `Surface´ indicates measurements conducted 0.5m above the water surface. Sunrise was at 04.49 GMT and sunset at 19.14 GMT (Nautical Almanac and Astronomical Ephemeris 1944).


a
K
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
0 2 4 6 8 10 12 14 16 18 20 22 24
Time (hours GMT)

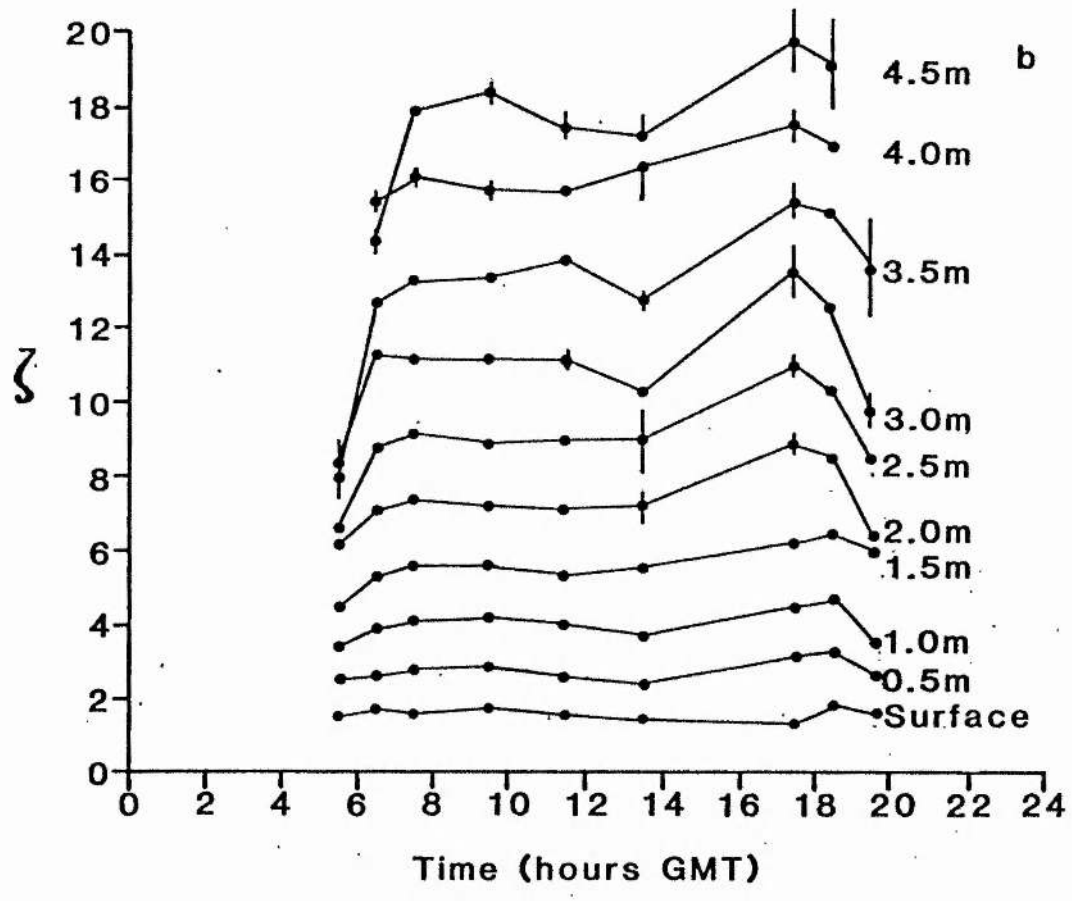
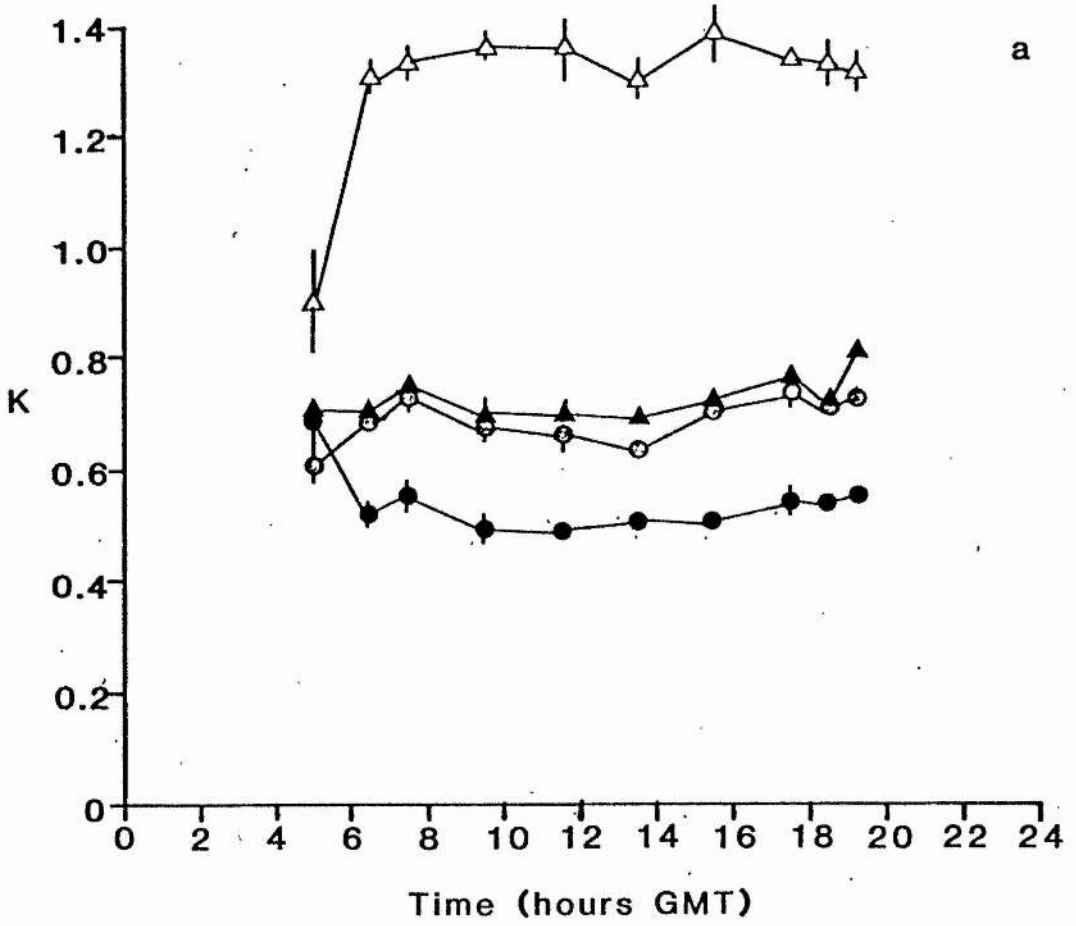

b
ζ
20
18
16
14
12
10
8
6
4
2
0
4.5m
4.0m
3.5m
3.0m
2.5m
2.0m
1.5m
1.0m
0.5m
Surface
0 2 4 6 8 10 12 14 16 18 20 22 24
Time (hours GMT)

Fig. 5.2. Diurnal change in the vertical diffuse attenuation coefficients (K_{PAR}, ▲, K_R, O, K_{FR}, △, K_R/K_{FR}, ●, ± S.E.) and ζ (± S.E.) in Loch Drumore on 9 April 1981. Sunrise was at 05.11 GMT and sunset at 18.53 GMT (Nautical Almanac and Astronomical Ephemeris 1944).


a
K
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
0 2 4 6 8 10 12 14 16 18 20 22 24
Time (hours GMT)

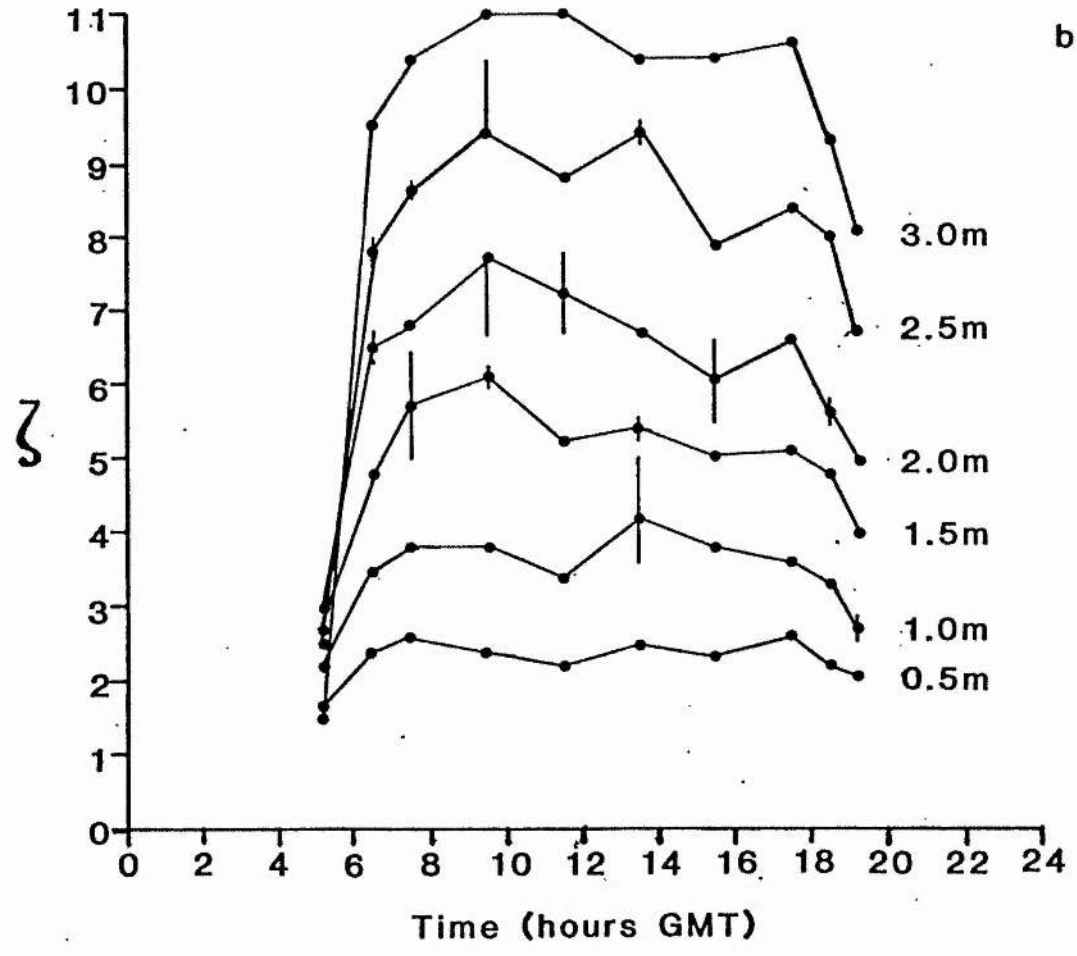
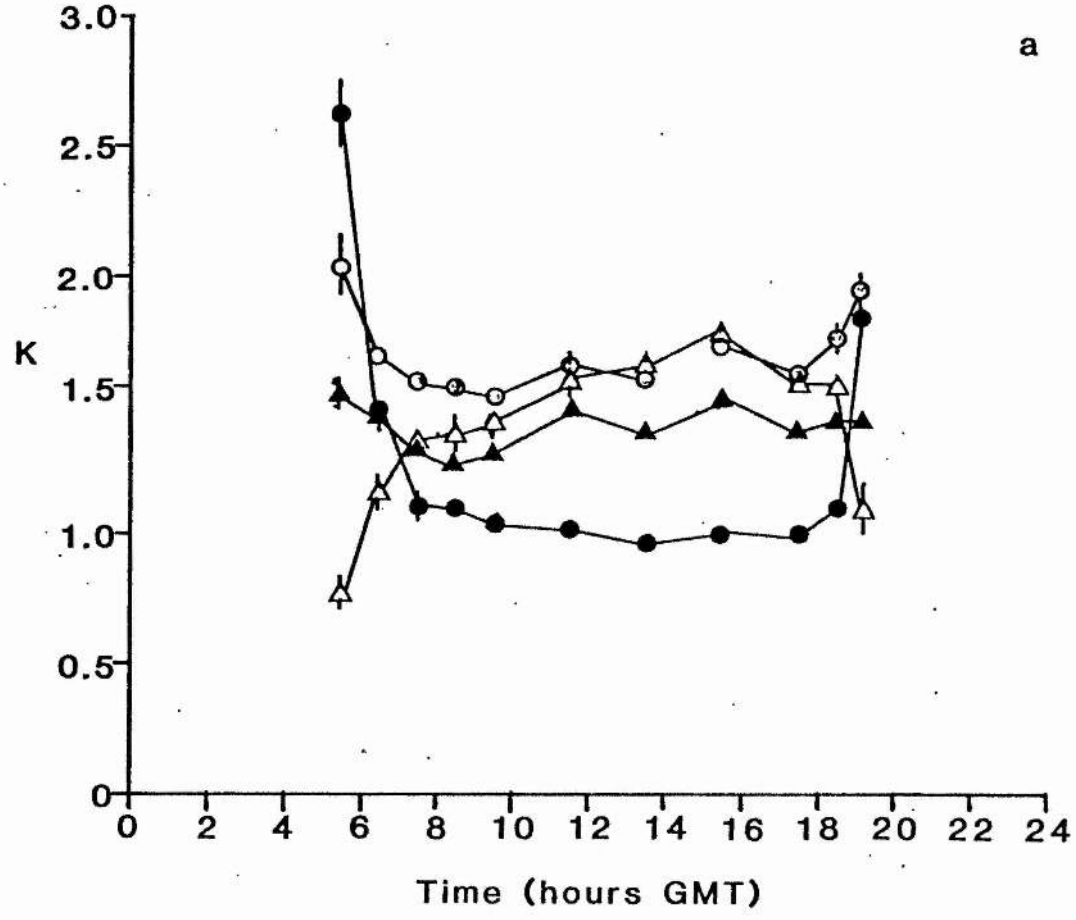

b
ζ
11
10
9
8
7
6
5
4
3
2
1
0
3.0m
2.5m
2.0m
1.5m
1.0m
0.5m
0 2 4 6 8 10 12 14 16 18 20 22 24
Time (hours GMT)

Fig. 5.3. Diurnal change in the vertical diffuse attenuation coefficients (K_{PAR}, ▲, K_R, ○, K_{FR}, △, K_R/K_{FR}, ●, ± S.E.) and ζ (± S.E.) in Fingask Loch on 17 April 1981. 'Surface' indicates measurements conducted 0.5m above the water surface. Sunrise as at 04.51 GMT and sunset at 18.09 GMT (Nautical Almanac and Astronomical Ephemeris 1944).


a
K
3.0
2.5
2.0
1.5
1.0
0.5
0
0 2 4 6 8 10 12 14 16 18 20 22 24
Time (hours GMT)

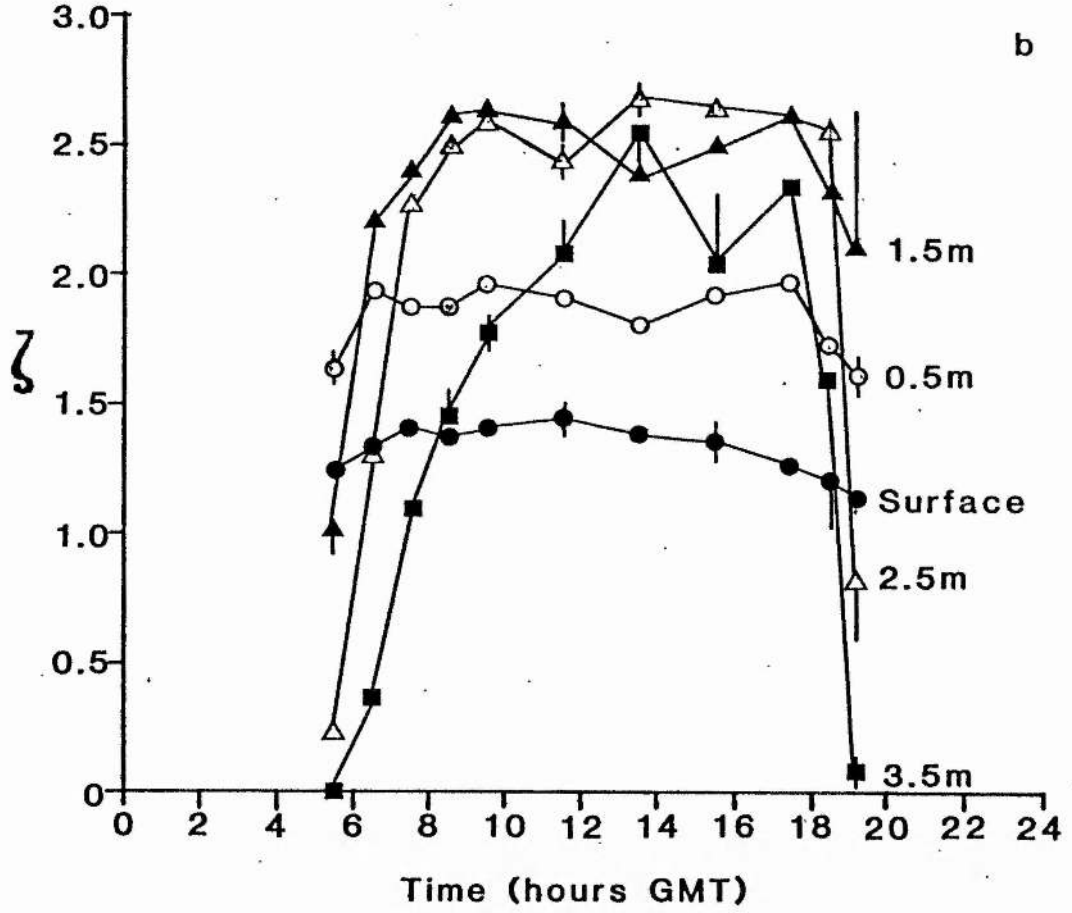
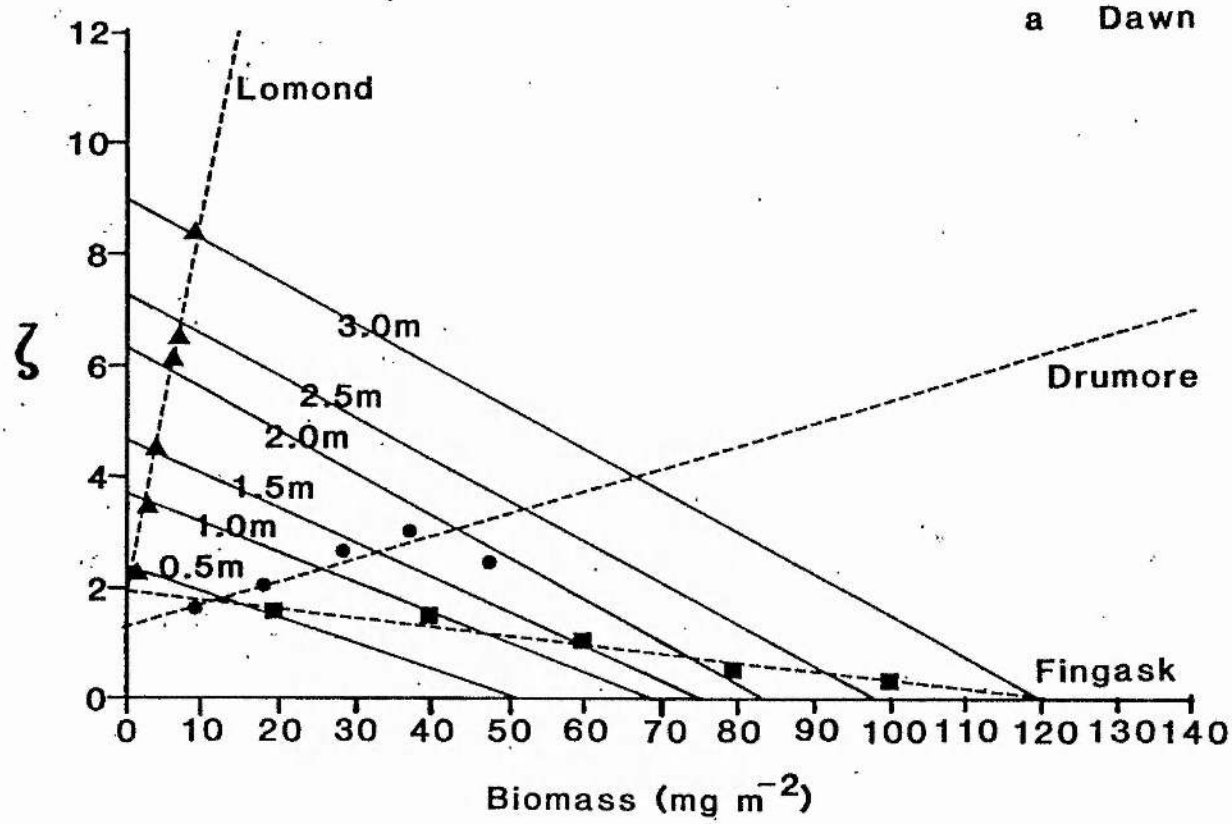

b
ζ
3.0
2.5
2.0
1.5
1.0
0.5
0
0 2 4 6 8 10 12 14 16 18 20 22 24
Time (hours GMT)
1.5m
0.5m
Surface
2.5m
3.5m

Fig. 5.4. ζ in relation to chlorophyll *a* biomass (the product of depth and chlorophyll *a* concentration) with depth in Loch Lomond, Loch Drumore and Fingask Loch at both dawn, (a), and midday, (b).


a Dawn
Lomond
Drumore
Fingask
3.0m
2.5m
2.0m
1.5m
1.0m
0.5m
ζ
0 10 20 30 40 50 60 70 80 90 100 110 120 130 140
0 2 4 6 8 10 12
Biomass (mg m⁻²)

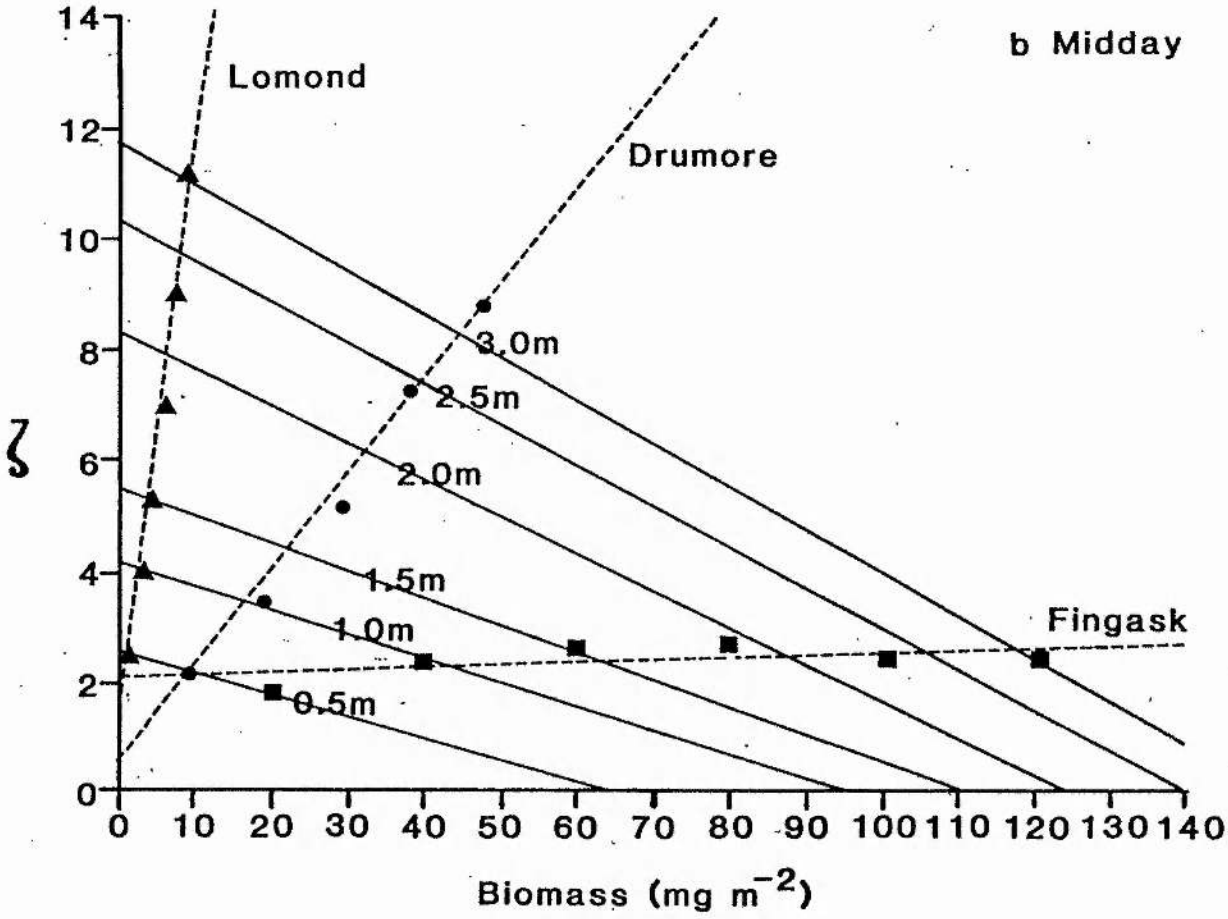
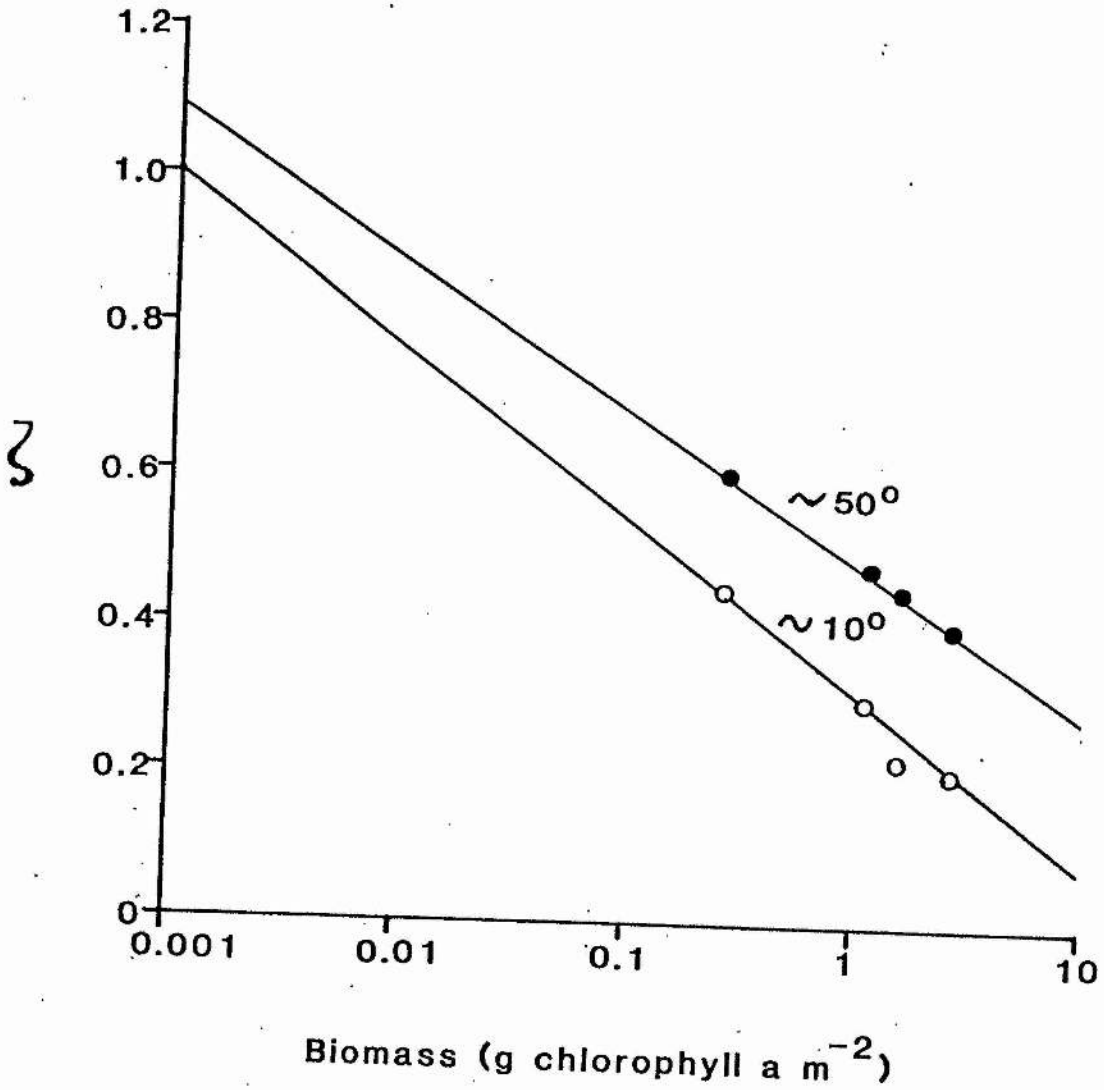

b Midday
Lomond
Drumore
Fingask
3.0m
2.5m
2.0m
1.5m
1.0m
0.5m
ζ
0 10 20 30 40 50 60 70 80 90 100 110 120 130 140
0 2 4 6 8 10 12 14
Biomass (mg m⁻²)

Fig. 5.5. ζ in relation to biomass in a wheat crop (Triticum aestivum) at low (~ 10°) and high (~ 50°) solar angles (after Holmes and Smith 1977b).


1.2
1.0
0.8
0.6
0.4
0.2
0
ζ
~50°
~10°
0.001
0.01
0.1
1
10
Biomass (g chlorophyll a m^{-2})

SECTION II

LABORATORY EXPERIMENTS

CHAPTER 6

PHOTOSYNTHETIC RATE - IRRADIANCE KINETICS

6.1 INTRODUCTION

The relationship between photosynthetic rate and PAR photon fluence rate, as graphically represented in a rate-irradiance curve, illustrates the dependence of the instantaneous rate of photosynthesis on the incident irradiance. Laboratory determinations of rate-irradiance curves provide well defined data on the photosynthetic characteristics of a population, not only in response to irradiance but also to such factors as nutrients and temperature, through their effect on the basic photosynthesis-light relationship. Thus, the determination of rate-irradiance curves for submerged macrophytes have formed an integral component of physiological investigations into growth responses (Steele 1962, Adams et al. 1974) and photosynthetic kinetics (Bowes et al. 1977a, Barko and Smart 1981), and ecological studies on productivity (Titus and Adams 1979) and distribution (Spence 1967, 1972, 1976, 1981, Spence and Chrystal 1970a, Agami et al. 1980).

Because rate-irradiance curves always exhibit a characteristic shape, numerous investigators have searched for a standard mathematical formulation which will describe the empirical relationship between photosynthesis and irradiance. Many researchers

of terrestrial systems have applied a rectangular hyperbolic function to rate-irradiance curves (Duncan et al. 1967, Shugart et al. 1974). In aquatic systems, Jassby and Platt (1976) determined that a hyperbolic tangent best represented the photosynthesis-light relationship for marine phytoplankton. However, the most representative mathematical model of rate-irradiance curves for submerged aquatic macrophytes has yet to be resolved.

The aim of the present study was twofold: to determine basic photosynthetic characteristics prior to physiological experimentation, and to conduct a preliminary investigation into the determination of a mathematical model for the relationship between photosynthesis and irradiance in P. crispus and P. obtusifolius.

6.2 RESULTS

Figures 6.1 and 6.2 illustrate the relationship between photosynthetic rate and the PAR photon fluence rate for freshly-collected shoots of P. crispus and P. obtusifolius, respectively. There was no significant difference ($p>0.05$) between photosynthetic rates of plants of the same species collected on the same date. These curves show the characteristic rate-irradiance relationship, whereby photosynthetic rate is linearly dependent upon the PAR fluence rate at low irradiance and independent at high (i.e. saturating) irradiance. The six curves presented here approach or attain P_{max}, the saturating photosynthetic rate. High irradiance

photoinhibition of photosynthesis was not measured.

For each species, the relationship between photosynthetic rate and irradiance is dependent upon collection date. Shoots of both P. crispus and P. obtusifolius collected on 15 August 1980 had the largest gross photosynthetic rates at every PAR fluence rate and appeared to require higher irradiances in order to attain P_{max}.

6.3 DISCUSSION

The relationship between photosynthetic rate and irradiance for any plant is highly dependent upon both the experimental conditions, specifically free CO_2 concentration and temperature, and the pretreatment conditions, particularly irradiance. Under experimental conditions of saturating irradiance, the photosynthetic rates of many submerged aquatic macrophytes are dependent upon the free CO_2 concentration, as determined by total carbon concentration and pH (Van et al. 1976, Bowes et al. 1977b, Allen and Spence 1981). The well-known inhibition of photosynthesis at high and low temperatures as symmetric about the temperature of maximum photosynthesis has also been observed (Barko and Smart 1981). In addition, many aquatic species can alter their photosynthetic capacity in response to pretreatment irradiance (Steele 1962, Spence and Chrystal 1970a, 1970b, Adams et al. 1974, Bowes et al. 1977b, Titus and Adams 1979, Barko and Smart 1981). Bowes et al. (1977b) and Barko and Smart (1981) reported that Hydrilla verticillata, pretreated at low

irradiance, adapted its photosynthetic and respiratory characteristics to more effectively use the lower light levels. Furthermore, plants pretreated at high irradiances have shown higher P_{max} values (Bowes et al. 1977b, Titus and Adams 1979), and Björkman et al. (1972) suggest that this may be due to greater activity of carboxydismutase and an increased capacity for light-saturated electron transport. Thus, the relationship between photosynthetic rate and irradiance is not inherently constant for a single plant, but is dependent upon its immediate past and present environmental conditions.

The variation in P_{max} between dates as reported here for both P. crispus and P. obtusifolius may reflect the irradiance conditions the plants were subjected to in the field, prior to collection. As there is no direct correlation between changes in P_{max} and collection date (hence, senescence), and as all photosynthetic measurements were conducted under standard conditions and at the lake temperature of 15°C, the high P_{max} values observed on 15 August 1980 for both species may have been due to prior exposure to high PAR fluence rates, caused by either a reduction in K_{PAR} or an increase in the incident irradiance.

The P_{max} values reported here for P. crispus are lower than the values of 0.8mmole O_2 g^{-1} h^{-1} reported by Allen and Spence (1981) and 2.39mmole O_2 g^{-1} h^{-1} reported by Gessner (1938 cited in Rabinowitch 1951), as recalculated assuming a 1:1 carbon:oxygen ratio and a specific leaf are of 1.5cm^{-2} mg^{-1} (Spence et al. 1973, Spence and Dale 1978). Similarly, Spence and Chrystal (1970a) reported higher P_{max} values of 1.29mmole O_2 g^{-1} h^{-1} for P. obtusifolius. However,

absolute comparisons of photosynthetic rates as measured by different investigators are difficult to interpret, not only because of the diversity in pretreatment and experimental conditions, but also because of the variety of techniques employed. In many studies, CO_2 uptake or liberation was used as the main criterion for characterizing photosynthetic or respiratory physiology (Bowes et al. 1977b, Titus and Adams 1979, Barko and Smart 1981). However, the evolution or consumption of O_2 may serve as a better index because aquatic plants, particularly those with an extensive lacunar system, show refixation of photorespired CO_2 (Søndergaard and Wetzel 1980). Large discrepancies in carbon uptake kinetics have also been observed between gas phase and liquid phase determinations, perhaps as a result of changes in fluid dynamics (Hough and Wetzel 1978, Søndergaard 1979). Furthermore, the use of a shoot, rather than a detached leaf (Van et al. 1976, Lloyd et al. 1977, Jana and Choudhuri 1979) or leaf discs (Lucas et al. 1978), can reduce the net photosynthetic rate per unit of photosynthesizing tissue due to the inclusion of such factors as stem respiration and self-shading of leaves.

Photosynthetic rate-irradiance curves play a central role in all theoretical studies of productivity. In order to conveniently and economically summarize the collection of data represented by a single rate-irradiance curve and to be able to make quantitative predictions about productivity, numerous investigators have attempted to fit these curves to a mathematical model. The most successful models have been:

1. the rectangular hyperbola, originally proposed by Baly (1935) and, because of its application in Michaelis-Menton rate-concentration relationships, the most extensively used

(e.g. Dugdale 1967, Duncan et al. 1967, Titus and Adams 1979, Allen and Spence 1981),

2. the non-rectangular hyperbola, proposed by Smith (1936) and Rabinowitch (1951),

3. the exponential model, as proposed by Steele (1962) and Crill (1977), and

4. the most recently proposed hyperbolic tangent (Jassby and Platt 1976).

To determine which of these four classes of models best expresses the relationship between photosynthetic rate and irradiance as reported here for P. crispus and P. obtusifolius the six graphs in Figures 6.1 and 6.2 were individually fitted to the following models, as recast by Jassby and Platt (1976) into a common form:

1. $P = P_{max}\alpha I / (P_{max} + I)$ (Baly 1935)
2. $P = P_{max}\alpha I / [(P_{max})^2 + (\alpha I)^2]^{\frac{1}{2}}$ (Smith 1936)
3. $P = \alpha I \exp(-\alpha I/P_{max}e)$ (Steele 1962)
4. $P = P_{max}\tanh(\alpha I/P_{max})$ (Jassby and Platt 1976)

where P_{max} is the saturating photosynthetic rate, P is the instantaneous photosynthetic rate at irradiance I, and α is the slope of the initial linear portion of the curve. These curves all employ gross photosynthesis, and thus the convention whereby the gross photosynthetic rate represents the sum of the net photosynthetic rate and the dark respiration rate, was followed although recent reports on photorespiration suggest this may not be justified (Jana and Choudhuri 1979).

The experimental data were fitted to the models and the `goodness of fit' was determined by the statistical methodology employed by Jassby and Platt (1976). α was calculated by linear regression on the low irradiance, linear portion of the rate-irradiance curve. P_{max} was then determined by substituting α into the equation and performing a non-linear least-squares fit to the model equation.

The `goodness of fit' (δ^2) for each model was determined as the mean squared deviation for the three curves for each species, namely:

$$\delta^2 = \frac{1}{3} \sum_{j=1}^{3} \sum_{k=1}^{m} (\hat{P}_{jk} - P_{jk})^2,$$

where P_{jk} is the measured photosynthetic rate for the j^{th} graph at the k^{th} irradiance, $\hat{P}_{jk}$ is the calculated photosynthetic rate, and m is the number of data points for the j^{th} curve.

P_{max} and α, as determined for the four equations and extrapolated from the graphs in Figures 6.1 and 6.2, are presented in Table 6.1 for both P. crispus and P. obtusifolius. On each date, P_{max} and α exhibited large variability between the different models. However, for both species, the rectangular hyperbola (Baly 1935) gave the best fit for the experimental data, according to the index δ^2 (Table 6.2). For ease of manipulation, the rectangular hyperbola is obviously the superior of the four models presented here. I_{comp}, the irradiance where net photosynthesis equals zero, can be easily calculated, unlike the other models which involve logarithmic or exponential terms. Although I_{max}, the irradiance at which P_{max} is

attained, can, theoretically, be calculated directly from the equation ($P = P_{max}$), P_{max} represents the maximum photosynthetic rate (calculated to two decimal places) that P approaches as I approaches infinity, and thus is not biologically meaningful.

Jassby and Platt (1976) compared eight rate-irradiance curves and determined that the hyperbolic tangent best described the empirical data from natural populations of marine phytoplankton. Smith (1936), Rabinowitch (1951), and Talling (1960a) also concluded that the rectangular hyperbola was one of the least successful representations of rate-irradiance curves.

Although the δ^2 values suggested that, on the average, the rectangular hyperbola (Baly 1935) best described the empirical data presented here, the most successful model for each of the three collection dates was not the rectangular hyperbola (Table 6.2). For both species, the rectangular hyperbola was the best model on 15 August 1980, whereas the hyperbolic tangent was most successful on 3 August 1980. The rectangular hyperbola also gave P_{max} values which were consistently larger than the observed.

Because of the difficulty in establishing a single mathematical formulation that will represent all rate-irradiance curves, Talling (1957a, 1957b) has adopted a standardized graphical approach which describes a curve by the intensity (I_k) at which a continuation of the initial linear gradient (α) would reach the light-saturated rate (P_{max}). The use of I_k, $I_k = P_{max}/\alpha$, to express the onset of light saturation of photosynthesis, is advantageous as it can be used on any

curve, regardless of its intrinsic curvature. Thus, the parameters P_{max}, I_{max}, and I_{comp}, as defined by Talling (1957a), serve as reliable tools for comparing photosynthetic characteristics between species and for assessing the effect of environmental factors on the rate-irradiance relationship.

However, one of the original goals of mathematical modelling was to facilitate quantitative predictions about productivity. In order to accomplish this goal, a successful mathematical model is still required. Thus, further measurements of photosynthetic kinetics for submerged macrophytes under standardized experimental and pretreatment conditions are necessary in order to determine whether a single mathematical model will successfully represent rate-irradiance relationships over a range of environmental conditions or whether, because of large variability in intrinsic curvature, a multi-factor model will be required in order to accurately predict productivity as a function of irradiance.

Fig. 6.1. The relationship between net photosynthetic rate (±S.E.) and PAR photon fluence rate at 15°C for fresh shoots of *P. crispus* collected from Loch Drumore on 3 August 1980, ● , 15 August 1980, ▲ , and 21 September 1980, ■ .

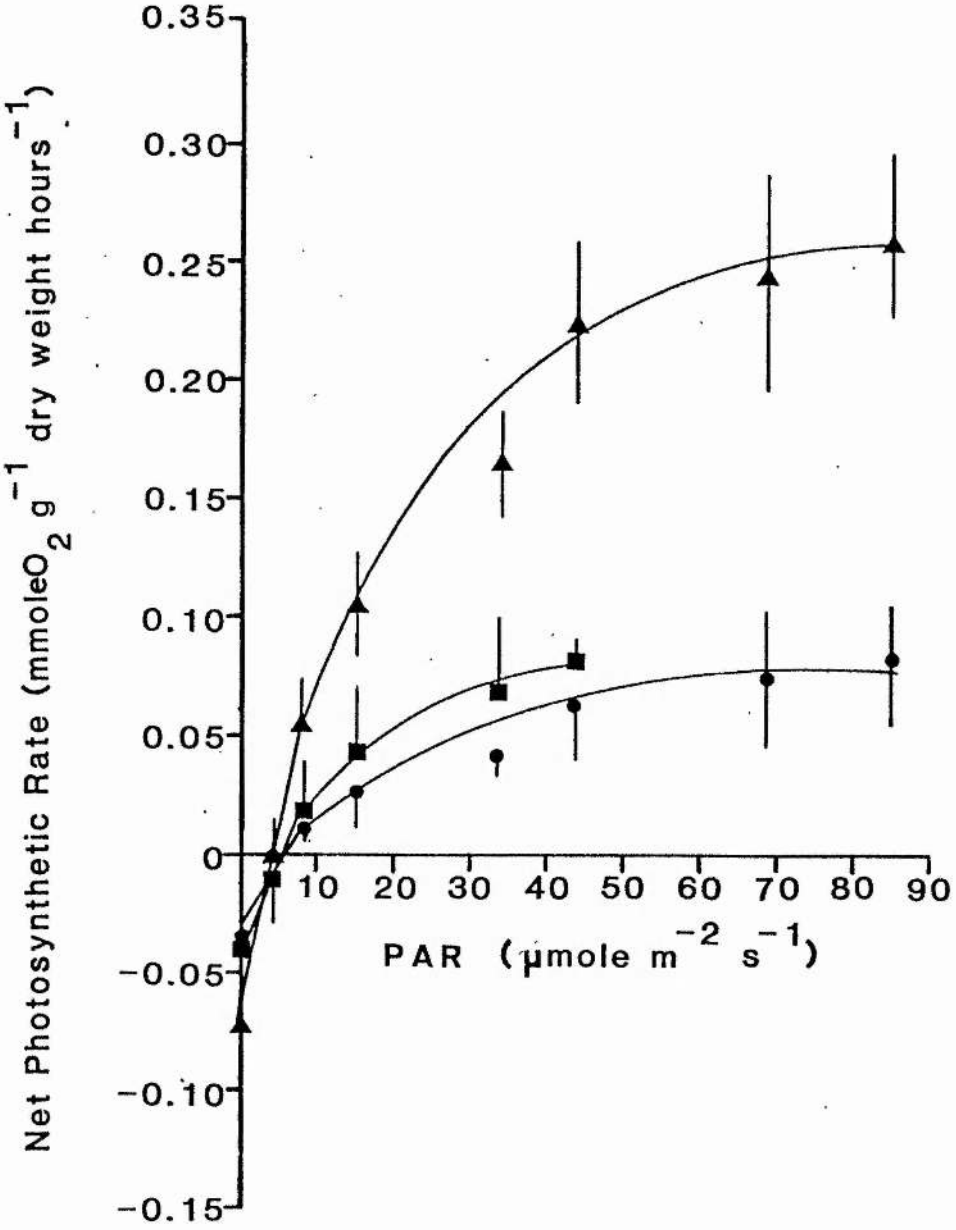

0.35
0.30
0.25
0.20
0.15
0.10
0.05
0
−0.05
−0.10
−0.15
10 20 30 40 50 60 70 80 90
PAR (μmole m^{-2} s^{-1})
Net Photosynthetic Rate (mmoleO_2 g^{-1} dry weight hours^{-1})

Fig. 6.2. The relationship between net photosynthetic rate (±S.E.) and PAR photon fluence rate at 15°C for fresh shoots of *P. obtusifolius* collected from Loch Drumore on 3 August 1980, ● , 15 August 1980, ▲ , and 21 September 1980, ■ .

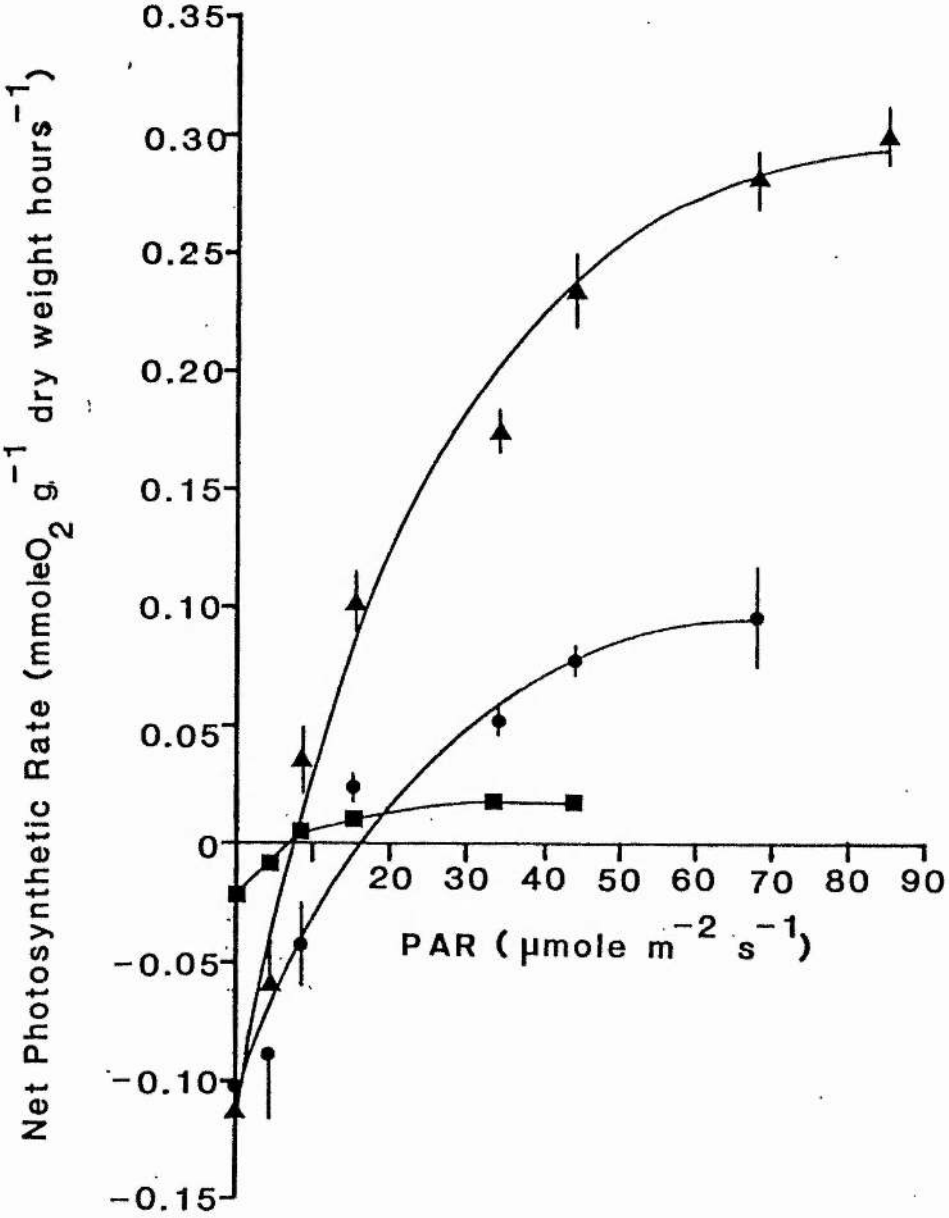

0.35
0.30
0.25
0.20
0.15
0.10
0.05
0
-0.05
-0.10
-0.15
20 30 40 50 60 70 80 90
PAR (µmole m^{-2} s^{-1})
Net Photosynthetic Rate (mmoleO_2 g^{-1} dry weight hours^{-1})

Table 6.1. The rate-irradiance parameters, Pmax and α, for P. crispus and P. obtusifolius as calculated from the original curves (Figures 6.1 and 6.2) and from four different mathematical models. Pmax represents the saturating gross photosynthetic rate (mmole O_2 g^{-1} h^{-1}) and α is the slope of the initial linear range of the curve at low PAR photon fluence rates. (See text for the mathematical equations.)

Collection Date	From Figure 6.1 and Figure 6.2		Rectangular Hyperbola		Non-rectangular Hyperbola		Exponential		Tan h	
	P_{max}	$\alpha x10^{-2}$	P_{max}	$\alpha x10^{-2}$	P_{max}	$\alpha x10^{-2}$	P_{max}	$\alpha x10^{-2}$	Pmax	$\alpha x10^{-2}$
P. crispus										
3.8.1980	0.13	0.65	0.16	0.63	0.12	0.63	0.13	0.63	0.11	0.63
15.8.1980	0.33	1.64	0.46	1.64	0.32	1.64	0.33	1.64	0.30	1.64
21.9.1980	0.13	0.70	0.20	0.73	0.12	0.73	0.12	0.73	0.11	0.73
P. obtusifolius										
3.8.1980	0.20	0.67	0.39	0.81	0.21	0.81	0.19	0.81	0.18	0.81
15.8.1980	0.41	1.80	0.57	1.92	0.40	1.92	0.40	1.92	0.37	1.92
21.9.1980	0.04	0.36	0.07	0.34	0.05	0.34	0.04	0.34	0.04	0.34

Table 6.2. Indices of 'goodness of fit' (δ^2) for the four mathematical models representing the photosynthetic rate - irradiance curves for freshly collected shoots of P. crispus and P. obtusifolius. The model which gave the best fit on each of the three collection dates is also shown.

	P. crispus		P. obtusifolius	
	δ^2	Best Fit (Date)	δ^2	Best Fit (Date)
Rectangular Hyperbola	1.06	15.8.1980	1.43	15.8.1980
Non-rectangular Hyperbola	1.33	21.9.1980	1.84	
Tan h	2.12	3.8.1980	2.83	3.8.1980 21.9.1980
Exponential	4.07		3.72	

CHAPTER 7

THE ENVIRONMENTAL CONTROL OF TURION PRODUCTION

7.1 INTRODUCTION

The induction of dormancy in many aquatic angiosperms occurs in response to short photoperiods, often in association with low temperatures. Plants of *Spirodela polyrrhiza* populations from north temperate regions formed turions under short photoperiods (Perry and Byrne 1969) and, although not strictly aquatic, the marsh plant, *Pinguicula grandiflora*, entered dormancy in response to short-day treatments (Heslop-Harrison 1962). Aiken (1976) observed that turion formation in natural populations of *Myriophyllum farwellii* coincided with decreasing photoperiods and high temperatures (greater than 20°C), while Weber and Nooden (1974) reported that low temperatures and short photoperiods were responsible for turion formation in *Myriophyllum verticillatum*. Dormancy induction by short days has also been observed in *Hydrocharis morsus-ranae* (Vegis 1953) and *Utricularia vulgaris* (Winston and Gorham 1979).

Phenological study of plants of *P. crispus* collected from a natural population revealed that turions were formed in July and August, when both photoperiod and temperature attained their yearly maximum, whereas turions were produced by *P. obtusifolius* in late August and September, when daylength was shorter. There was no obvious relationship between PAR photon fluence rate or light quality

and turion production in either P. crispus or P. obtusifolius. Thus, dormancy induction in these species may also be regulated by photoperiod and temperature.

However, field studies, although serving to identify the possible environmental variables triggering a particular morphological response, rarely permit controlled manipulation of environmental parameters. Therefore, the objective of the present study was to determine, through controlled laboratory experiments, the role of environmental factors, such as temperature and photoperiod, on dormancy induction in P. crispus and P. obtusifolius.

7.2 RESULTS

Turion production by P. crispus under long-day conditions was dependent upon temperature (Fig. 7.1). Turions were not produced at experimental temperatures below 15°C; the critical temperature, as extrapolated from the graph, was about 16°C. Temperatures above the critical were associated with a corresponding increase in the turion index and a reduction in the time to visible turion formation. Plants grown at 35°C produced few turions; these shoots rapidly died and new shoots were not initiated from the rhizome.

At the optimum temperature (30°C), turion index and the time to visible turion formation in P. crispus was dependent upon photoperiod (Fig. 7.2). Turions were not produced by plants under photoperiodic treatments of less than or equal to 12h; the critical daylength was between 12 and 16h. Maximum turion production and minimum time until turion appearance was observed under an 18h photoperiod.

Under optimal temperature (30°C) and photoperiodic (18h) conditions, turion production by P. crispus was also dependent upon the PAR photon fluence rate (Fig. 7.3). Time to visible turion formation was inversely proportional to PAR fluence rate, whereas the turion index showed a direct relationship.

Turion production was not related to the total daily light level (the total radiant energy expressed as the product of the PAR photon fluence rate and photoperiod), as illustrated in Fig. 7.4. Plants under long day conditions always produced turions, whereas plants under short day treatments, although exposed to higher total daily light levels than plants under some long day treatments, never formed turions. Plants of P. crispus, when grown under short day conditions in 0.3 or 0.6mM sucrose solutions, produced luxuriant vegetative growth yet no turions (Table 7.1).

Under optimum conditions for dormancy induction (30°C temperature, 18h photoperiod, 400μmole m^{-2} s^{-1} PAR), turion production by P. crispus was dependent upon ζ (Fig. 7.5). Turion index was minimal at a ζ value of 1.0 and maximal at a ζ value of 2.3. There was no significant difference ($p>0.05$) between the turion indices of

plants exposed to ζ values of 2.3, 12 or 24. Time to visible turion formation was inversely proportional to ζ for ζ values of less than about 8.

Pretreatment under inductive long day and high temperature conditions prior to transference to non-inductive conditions demonstrated that only one inductive photoperiod, whereas several inductive thermoperiods, were required for turion formation in P. crispus (Fig. 7.6). Plants transferred to low temperature conditions rarely, if ever, produced turions although they had been exposed for a maximum of five days to inductive light and temperature pretreatment conditions. However, plants maintained at high temperatures throughout the experiment formed turions in response to only one inductive photoperiod. There was no significant difference ($p \geq 0.05$) between the turion indices of plants pretreated for one to five days and maintained at high temperatures.

P. crispus failed to produce turions when grown at 30°C under a 10h photoperiod with a one hour R night-break, and plants growing in a 0.3mM sucrose solution under a 10h photoperiod at 30°C produced luxuriant vegetative growth but no turions (Table 7.1). However, when the main photoperiod was extended from 10h to 12h (still a noninductive daylength), the addition of a one hour R night-break resulted in the formation of turions (Table 7.1).

Turions were also produced by plants grown at 30°C under a 10h photoperiod which was extended with an additional 8h of R or FR low fluence light, however the R end-of-day extension was not as effective for dormancy induction (Table 7.1). The turion index and time to visible turion formation for plants exposed to a 20μmole m^{-2} s^{-1} FR end-of-day extension was dependent upon the sucrose concentration of the ambient solution (Fig. 7.7). Turions were produced most rapidly and in the largest quantity by plants in a 0.6mM sucrose solution. Increasing the photon fluence rate of the FR end-of-day extension did not increase either the turion index or the time to visible turion formation for plants in 0.6mM sucrose solutions (Table 7.2).

A preliminary experiment was conducted on the photoperiodic and temperature control of turion production in P. obtusifolius. Of the four experimental treatments, which combined either a long day (18h) or a short day (10h) with either a high (25°C) or low (15°C) temperature, only plants at 25°C under short day conditions produced turions.

7.3 DISCUSSION

Unlike other temperate climate aquatic angiosperms, dormancy induction in P. crispus is triggered in response to long days and high temperatures. Under laboratory conditions, a critical temperature of about 16°C and a critical daylength of between 12 to

16h was determined. Turion production was maximal at a temperature of 30°C and a photoperiod of 18h. Recent laboratory investigations by Sastroutomo (1980) also confirm the role of temperature and photoperiod on turion formation in P. crispus.

In contrast, turions were produced by P. obtusifolius in response to short days and high temperatures. Natural populations of Myriophyllum farwellii and Utricularia vulgaris were also observed to form turions during periods of high temperature and decreasing day length (Aiken 1976, Winston and Gorham 1979). However, controlled experiments on U. vulgaris showed that short days were the trigger for turion formation and that this response was enhanced by concomitant low temperatures (Winston and Gorham 1979).

Laboratory experiments have shown that turions of Hydrocharis morsus-ranae are formed in response to short days and high temperatures (Vegis 1953). At 10°C and independent of day length, turions were never produced. At high temperatures (15 to 25°C), turions were produced only under short day conditions, however as the temperature increased, the critical daylength permissive to turion induction also increased. Thus, at very high temperatures turion production was independent of daylength. Temperature was, therefore, the primary determinant of dormancy induction in H. morsus-ranae.

Turion formation in both P. crispus and P. obtusifolius is apparently more sensitive to the combined effects of temperature and photoperiod than was shown for U. vulgaris (Winston and Gorham 1979) and H. morsus-ranae (Vegis 1953). Neither inductive temperatures nor inductive photoperiods could independently induce turion formation in either species.

The long photoperiods triggering turion production in P. crispus may be perceived by a response to light quantity (for example a photosynthetic response), light quality (for example a phytochrome-mediated response), or by an integrated response to both light quantity and quality. A photosynthetic pathway signifies that a theshold concentration of photosynthate is required before turion formation can be initiated. The rate of turion production and the number of turions per shoot may or may not be dependent upon photosynthate concentration above the threshold level, depending upon whether photosynthate concentration exhibits a quantitative, as well as a qualitative, effect.

In plants of Spirodela polyrrhiza, turion formation is dependent upon a balance being reached between the PAR photon fluence rate and temperature such that photosynthetic production exceeds respiration demands and an excess of photosynthate is accumulated (Jacobs 1947, Czopek 1963, 1964, Newton et al. 1978, Krajncic and Devide 1980). The relationship between PAR photon fluence rate and turion production in P. crispus under inductive conditions may, at first, suggest that turion production is dependent solely upon photosynthate

concentration. However, turions were produced on shoots grown at both low PAR photon fluence rates and low total daily light levels, implying that a threshold photosynthate concentration, per se, was not responsible for turion formation. Furthermore, plants under short day conditions (10 or 12h at 400μmole m^{-2} s^{-1} PAR) failed to produce turions although total daily light levels were greater than those of some long day treatments (18h at 60 or 100μmole m^2 s^{-1}) under which turions were produced. Likewise, plants grown under short day conditions in 0.3 and 0.6mM sucrose solutions produced luxuriant vegetative growth yet no turions. Thus, the long days triggering turion formation in P. crispus are not acting through a photosynthetic mechanism. However, under inductive conditions, photosynthate concentration, and hence PAR photon fluence rates, may exert a quantitative effect, determining both the rate of turion production and turion index.

An alternate means of perceiving daylength is through the action of phytochrome. Phytochrome has been shown to exhibit two main types of action: the static mode of action, also termed the low energy, low irradiance or induction response, and the dynamic mode of action, also called the high energy, high irradiance, or cycling response (Fredericq 1972, Smith 1975, Jose and Vince-Prue 1978, Mancinelli and Rabino 1978). Light responses operating through the static mode of action are dependent upon light quality, and are characterized by R-FR reversibility, whereby the response is triggered by exposure to a brief pulse of low energy R light (660nm) and is inhibited by a subsequent exposure to a brief pulse of FR light (730nm). In continuous irradiation with broad band sources absorbed by both Pr and

Pfr, the magnitude of the response is determined by the photoequilibrium proportion of Pfr, represented by φ (the ratio of Pfr to Ptotal), which is quantitatively related to ζ (Morgan and Smith 1976, Holmes and Smith 1977b, Frankland and Letendre 1978).

Light responses operating through the dynamic mode of action are dependent upon both light quantity and quality, requiring prolonged exposure to high irradiance, showing strong irradiance dependency and no photoreversibility, and exhibiting an action spectrum peak between 710 and 730nm (Mancinelli and Rabino 1978). The dynamic mode of action does not appear to operate through the form of phytochrome that mediates the static mode, but is dependent upon the rate of cycling, as determined by fluence rate, between Pfr and an excited or associated state of Pfr (Schafer 1975, Jose and Vince-Prue 1978).

Most photoperiodic responses are associated with the static mode of phytochrome action, and the inductive long days triggering turion formation in P. crispus exhibit static mode characteristics. The magnitude and the response time for turion production under inductive conditions are both dependent upon ζ, usually characteristic of the static mode of action. The expression of a morphological response after only one inductive photoperiod is also consistent with the static mode of phytochrome action.

The classic test for implicating the static mode of phytochrome action in a photoperiodic phenomenon is the expression of the morphological trait in response to a dim R night-break during a non-inductive photoperiod. Turions were produced by P. crispus when

grown at 30°C under a 12h photoperiod with a one hour R night-break. Thus, the photoperiodic control of turion formation in P. crispus, as mediated by the static mode of phytochrome action, is confirmed.

Turions were not produced by plants under a 10h photoperiod with a one hour R night-break. Under identical conditions, the addition of 0.3mM sucrose resulted in luxuriant vegetative growth yet no turions. Thus, the hypothesis that insufficient photosynthate may be quantitatively limiting turion production under a 10h day with a R night-break proved false. Hordeum vulgare and Hyoscyamus niger, the species for which the original action spectrum for flowering in long day plants was determined, also failed to respond to a brief R night-break in the middle of a 16h, rather than a 12h, dark period (Lane et al. 1965). The reason for this is not fully understood, although it may due to an inability to entrain an endogenous developmental rhythm with diurnal changes in the optimum φ necessary for induction (Vince-Prue 1975).

P. crispus plants grown at 30°C under 10h photoperiods which were extended with an additional 8h of R or FR low fluence light were also capable of turion production, however fewer turions were produced under the R end-of-day extension. The stimulatory effect of FR, as opposed to R light, suggests that the dynamic mode of phytochrome action may also perceive the inductive long days. However, the end-of-day PAR photon fluence rate appears too low to establish Pr-Pfr cycling, as fluence rates greater than 45μmole m^{-2} s^{-1} are usually required for operation of the dynamic mode of action (Mancinelli and Rabino 1972). Furthermore, at an ambient temperature of 15°C, the PAR

compensation fluence rate for P. crispus shoots was 5μmole m^{-2} s^{-1} (Fig. 6.1), and as the present experiment was conducted at 30°C, the 20μmole m^{-2} s^{-1} PAR photon fluence rate of the end-of-day extension probably approached the light compensation point. Increasing the PAR photon fluence rate of the FR end-of-day extension increased neither the turion index nor the response time, thus discounting involvement of the dynamic mode of phytochrome action.

The poorer performance by plants exposed to R, as opposed to FR light, is contradictory to the earlier observation that Pfr is required at the end of the long day for maximum turion production. The weak response to the R end-of-day extension may have been caused by the screening effect of chlorophyll, which reduces the R fluence rate and may thereby prevent complete photoconversion of the phytochrome signal (Jose et al. 1977, Ohtani and Kumagi 1980). Spence (1981) showed that the leaf attenuation coefficients for a fresh green leaf of P. crispus were 1.08 and 0.26 for $K_{R(leaf)}$ and $K_{FR(leaf)}$, respectively. Thus, R light was attenuated almost five times more quickly than FR light as it passed through a leaf. However, the plants were able to perceive the R night-break, which had a PAR photon fluence rate of 25μmole m^{-2} s^{-1}, only 5μmole m^{-2} s^{-1} greater than the R end-of-day extension. Thus, it is unlikely that the R end-of-day extension was too weak to establish phytochrome photoequilibrium.

When day extensions following a short day in sunlight were used to induce flowering in long day plants, a mixture of R and FR light frequently produced a much greater response than R light alone (Lane et al. 1965, Vince 1965, Vince-Prue 1975), although FR light had little or no effect when added to a night-break (Vince 1969). In Hyoscyamus niger, the action spectrum for long night-breaks was found to differ from the characteristic static mode of phytochrome action, in that peak activity occurred at 710nm for light given for 8h over the middle of a daily 16h dark period (Schneider et al. 1967 cited in Vince-Prue 1975), while a 15 minute night-break showed an action peak between 600 to 660nm (Parker et al. 1950). The reason for the enhanced response when FR light is added to a R end-of-day extension is still uncertain, however it may also be due to unsuccessful entrainment of an endogenous rhythm with diurnal changes in the optimum φ necessary for induction (Vince-Prue 1975).

The rate of production and number of turions for P. crispus plants grown under short days with a FR end-of-day extension was also dependent upon the sucrose concentration of the ambient solution. Turion production was maximal at a sucrose concentration of 0.6mM, however modifying the present experiment, so as to reduce the increment between the investigated sucrose concentrations, may have shown that turion indices at high and low sucrose concentrations were symmetric about an optimum sucrose concentration, which was between 0.6 and 3.0mM. The time until visible turion formation did not decrease for sucrose concentrations greater than 0.6mM, suggesting that although higher sucrose concentrations may increase the turion

index, visible turion development never occurs until 10 to 12 days after the onset of inductive conditions. Thus, sucrose concentration controls the magnitude and rate of turion production, but not the actual induction of dormancy.

Soluble carbohydrate levels have also been shown to exert a strong influence on phytochrome-mediated responses in other plants. Gaudet (1963) showed that in Marsilea vestita the transition from the aquatic to the terrestrial form was dependent upon FR light, and that the critical length of the FR exposure was inversely proportional to the sucrose concentration of the medium. Larpent-Gourgard and Aumaitre (1980) reported that the position of lateral branch buds in the protonema of the bryophyte, Ceratodon purpureus, was controlled by the photoperiodic action of phytochrome, and that the latter could only operate when sufficient photosynthate was present. Thus, photosynthate may be required as a substrate before a photoperiodic reaction can be initiated and/or it may control the magnitude of the phytochrome-mediated response.

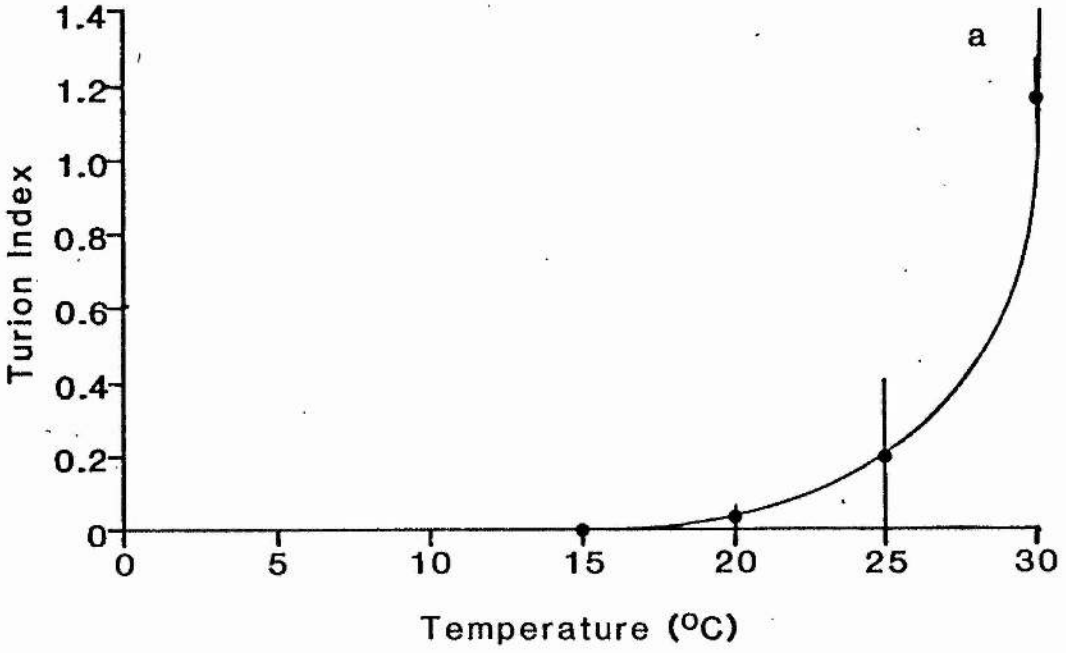
In P. crispus, photosynthate concentration exhibits a quantitative influence on turion production, determining both number and rate of turion production under inductive conditions of long days and high temperatures. The long days represent a photoperiodic signal which is perceived by phytochrome operating through the static mode of action and trigger the induction of dormancy. However, the PAR photon fluence rate, by determining the photosynthate concentration, controls the magnitude of the response. These environmental stimuli ensure that P. crispus enters dormancy around midsummer, in direct contrast

to other temperate climate aquatic angiosperms. The only other group of angiosperms in which a long photoperiod at high temperatures induces the formation of perennating organs are the steppe perennials, such as Allium cepa, A. sativum. A. ascalonicum and A. proliferum, which are adapted to a climate with a hot arid summer (Jenkins 1954, Reimers 1957, 1958 cited in Vegis 1964). Summer dormancy in P. crispus may likewise represent an adaptive strategy to avoid the high respiratory demands associated with summer temperatures and the competition with phytoplankton and other macrophytes for nutrients and light.

Fig. 7.1. Effect of temperature on turion production in P. crispus. Experimental conditions: 18h photoperiod, 400μmole m^{-2} s^{-1} PAR, and ζ=12.

a. Turion Index

b. Number of days until turions first observed. (Turions were not produced at 15°C.)


a
Turion Index
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
0
5
10
15
20
25
30
Temperature (°C)

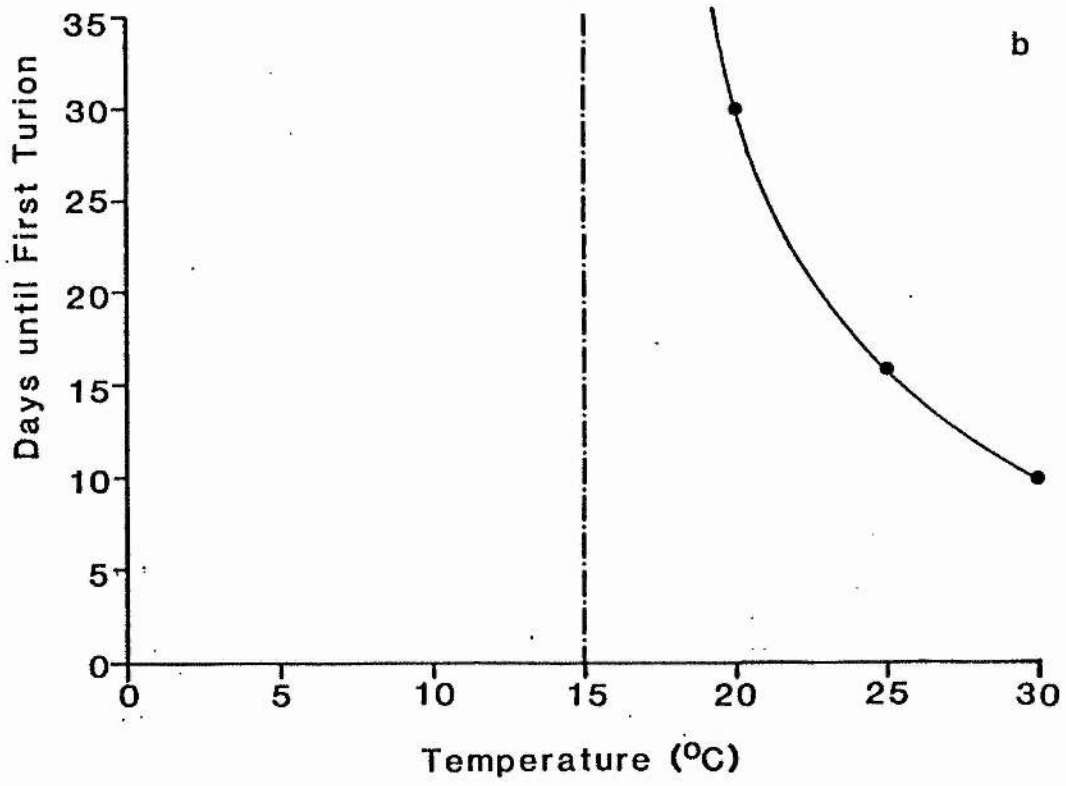
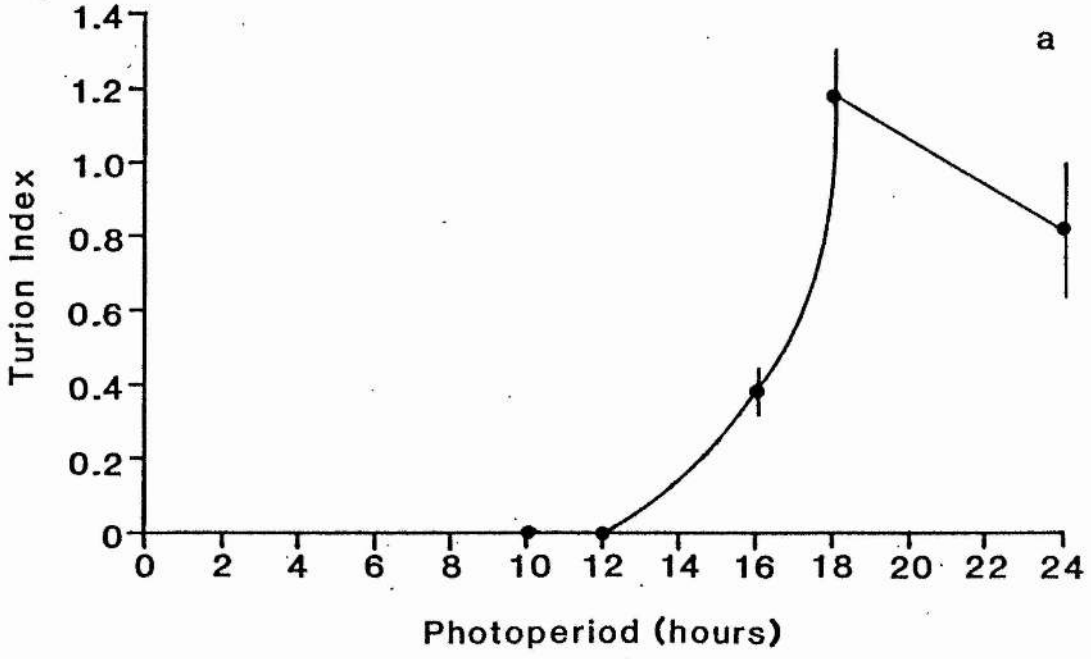

b
Days until First Turion
35
30
25
20
15
10
5
0
0
5
10
15
20
25
30
Temperature (°C)

Fig. 7.2. Effect of photoperiod on turion production in P. crispus. Experimental conditions: 30°C temperature, 400μmole m^{-2} s^{-1} PAR, and ζ =12.

a. Turion Index

b. Number of days until turions first observed. (Turions were not produced under 10 and 12h photoperiods.)


a
Turion Index
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
0 2 4 6 8 10 12 14 16 18 20 22 24
Photoperiod (hours)

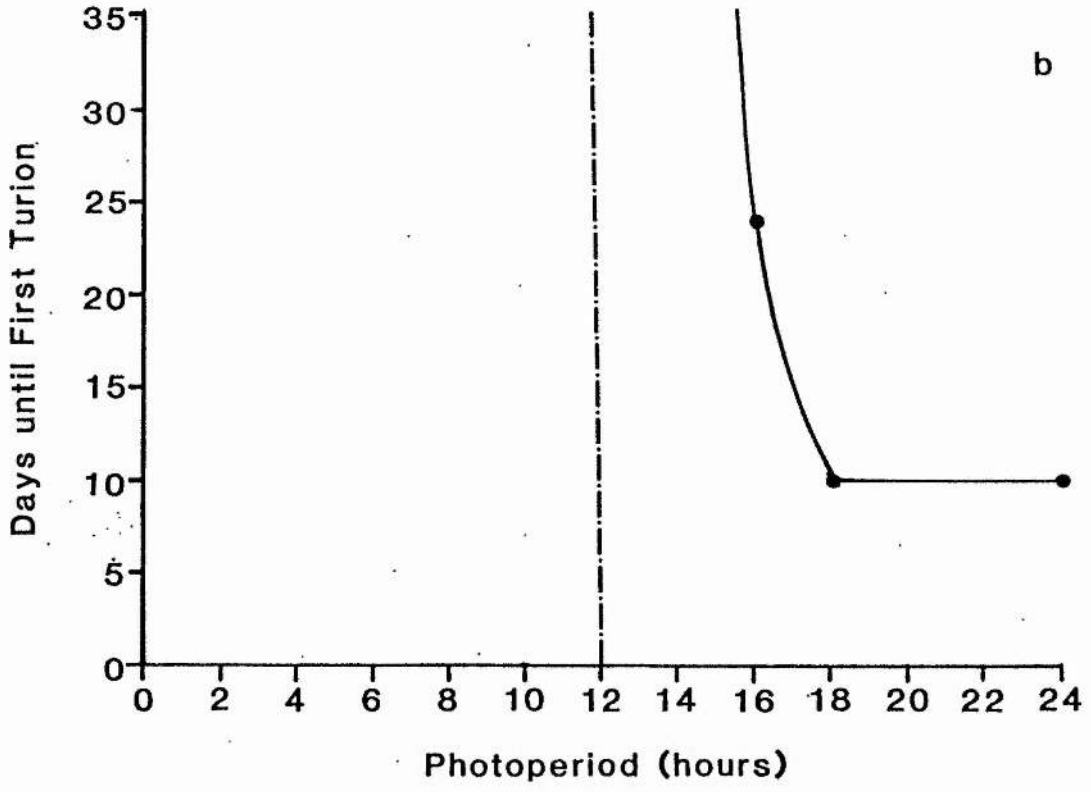
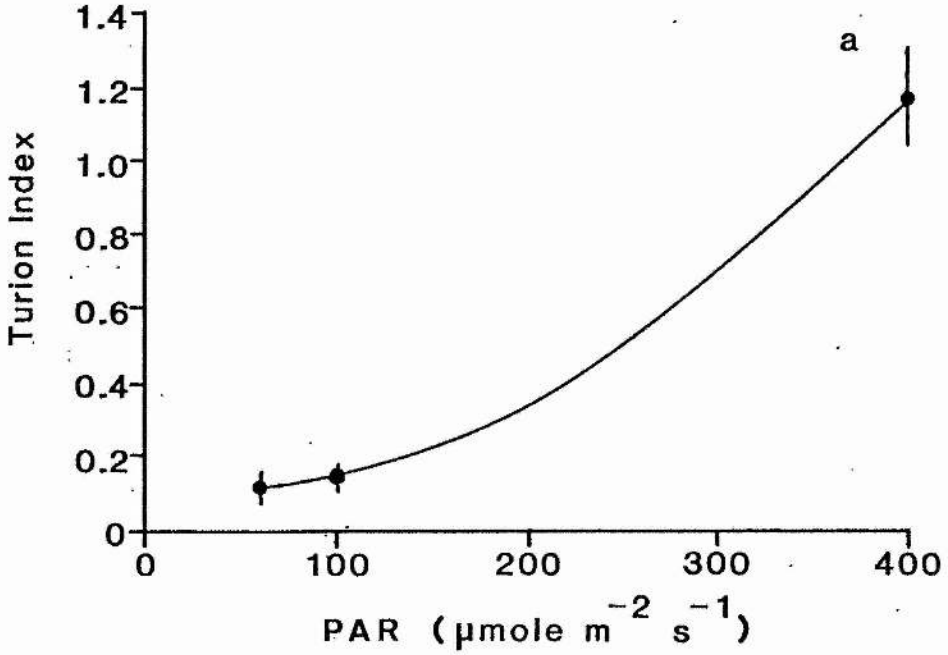

b
Days until First Turion
35
30
25
20
15
10
5
0
0 2 4 6 8 10 12 14 16 18 20 22 24
Photoperiod (hours)

Fig. 7.3. Effect of PAR photon fluence rate on turion production in P. crispus. Experimental conditions: 30°C temperature, 18h photoperiod, and ζ=12.

a. Turion Index

b. Number of days until turions first observed.


a
Turion Index
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
0
100
200
300
400
PAR (μmole m^{-2} s^{-1})

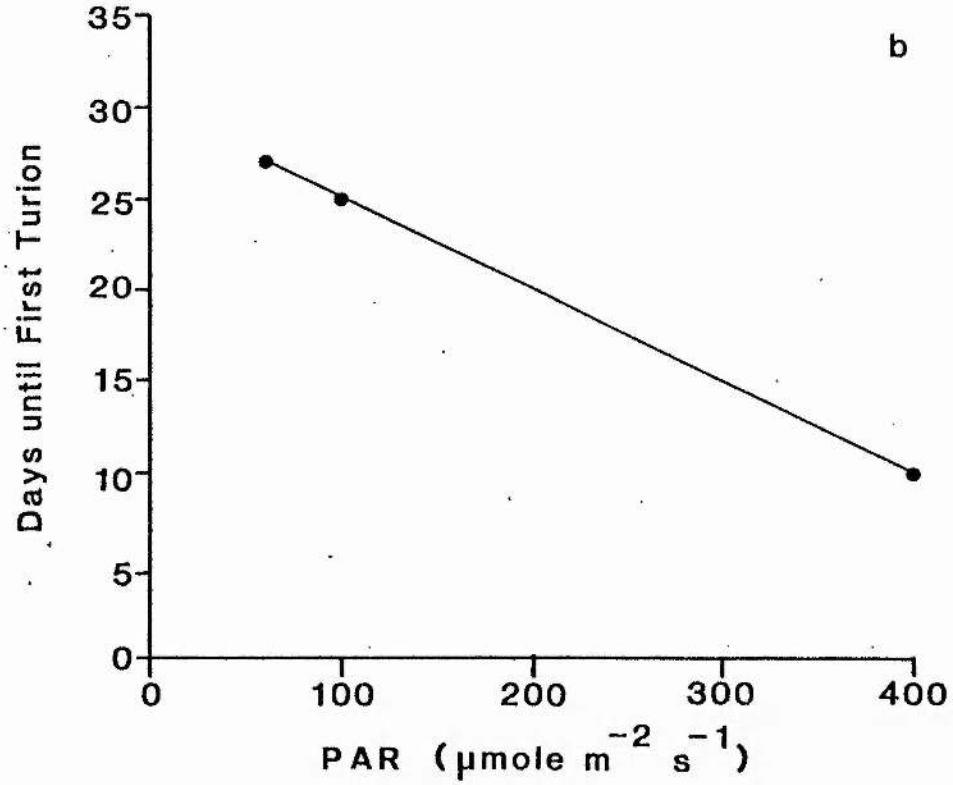
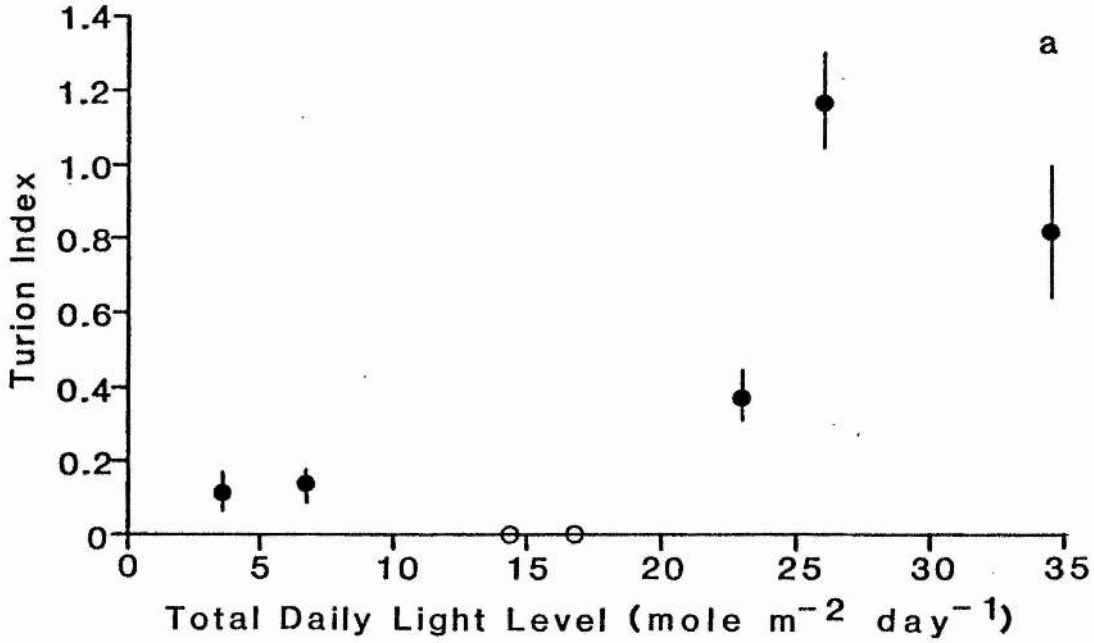

b
Days until First Turion
35
30
25
20
15
10
5
0
0
100
200
300
400
PAR (μmole m^{-2} s^{-1})

Fig. 7.4. Effect of total daily light level (the product of the PAR photon fluence rate and the photoperiod) on turion production in P. crispus. Plants were grown under either short day treatments (10 or 12h), O , or long day treatments (greater than 16h), ● . Experimental conditions: 30°C temperature, and ζ=12.

a. Turion Index

b. Number of days until turions first observed. (Turions were not produced under short days.)


a
Turion Index
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
0
5
10
15
20
25
30
35
Total Daily Light Level (mole m^{-2} day^{-1})

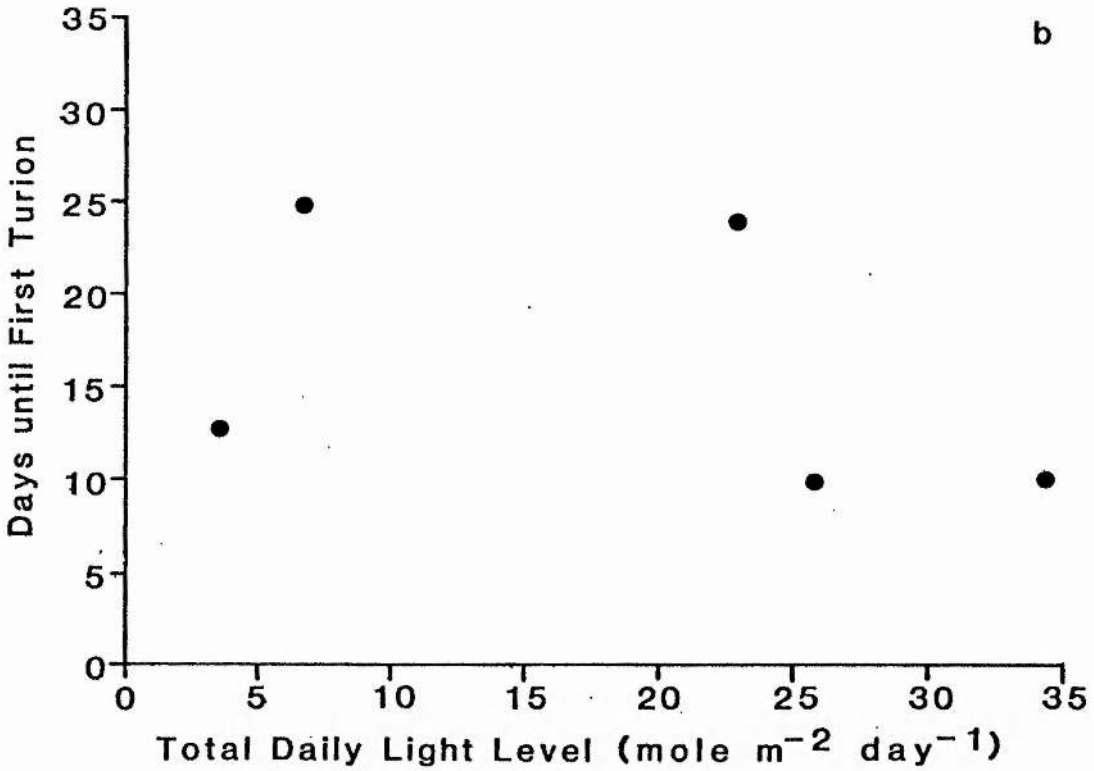
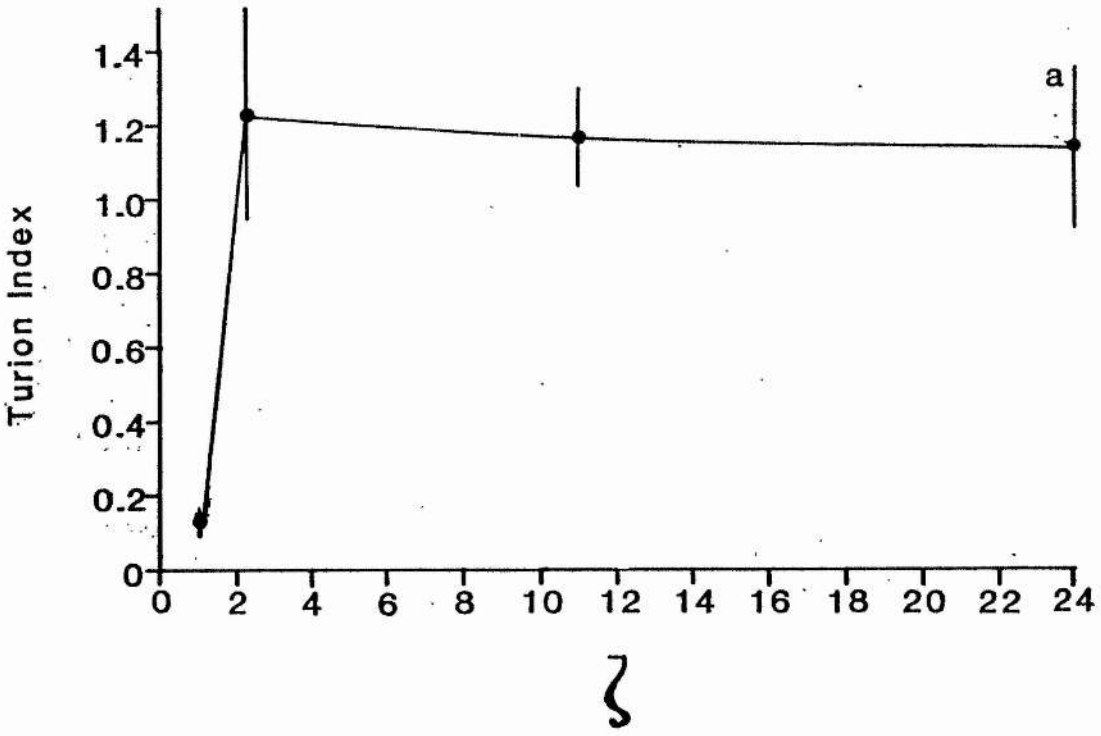

b
Days until First Turion
35
30
25
20
15
10
5
0
0
5
10
15
20
25
30
35
Total Daily Light Level (mole m^{-2} day^{-1})

Fig. 7.5. Effect of ζ on turion production in P. crispus. Experimental conditions: 30°C temperature, 18h photoperiod, and 400μmole m^{-2} s^{-1} PAR.

a. Turion Index

b. Number of days until turions first observed.


Turion Index
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
0 2 4 6 8 10 12 14 16 18 20 22 24
a

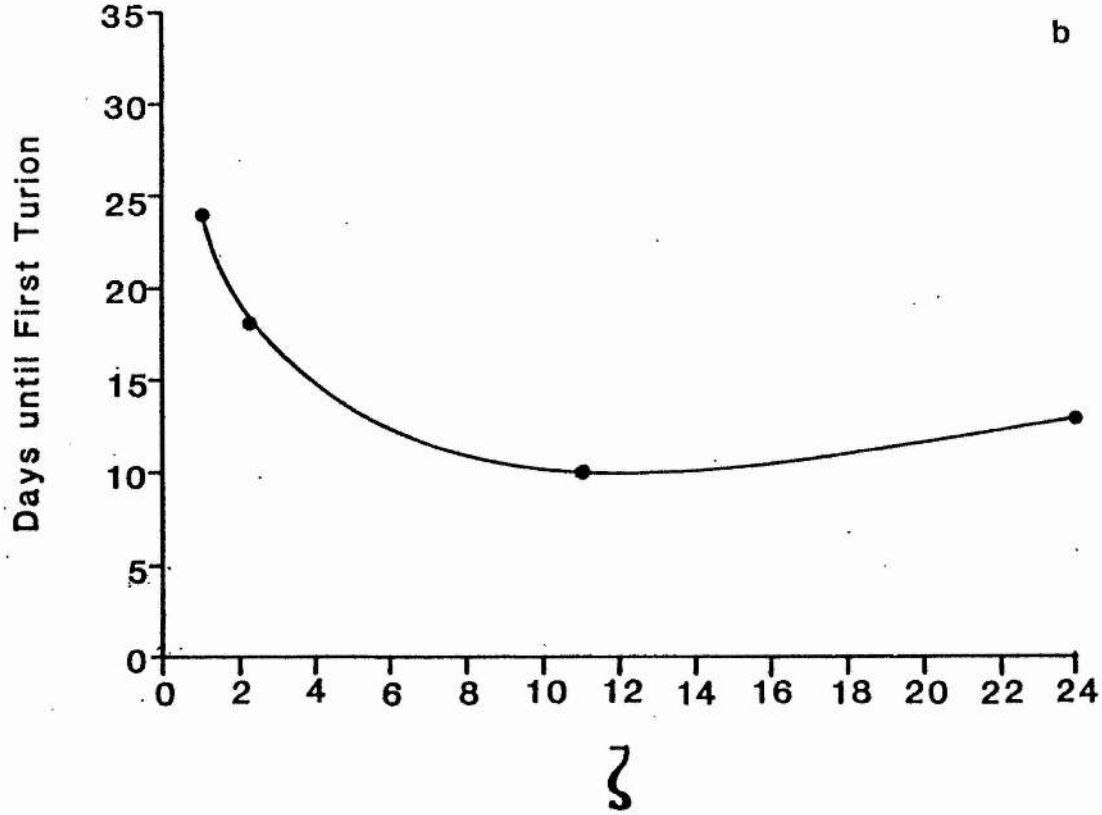

Days until First Turion
35
30
25
20
15
10
5
0
0 2 4 6 8 10 12 14 16 18 20 22 24
b

Fig. 7.6. Effect of pretreatment under inductive conditions (30°C temperature, 18h photoperiod, 400μmole m^{-2} s^{-1} PAR, ζ=12) prior to transference to non-inductive conditions of long days (18h) at 15°C, ●, short days (10h) at 15°C, △ , or short days (10h) at 30°C, ○ . Non-inductive experimental conditions: 400μmole m^{-2} s^{-1} PAR, and ζ=12.

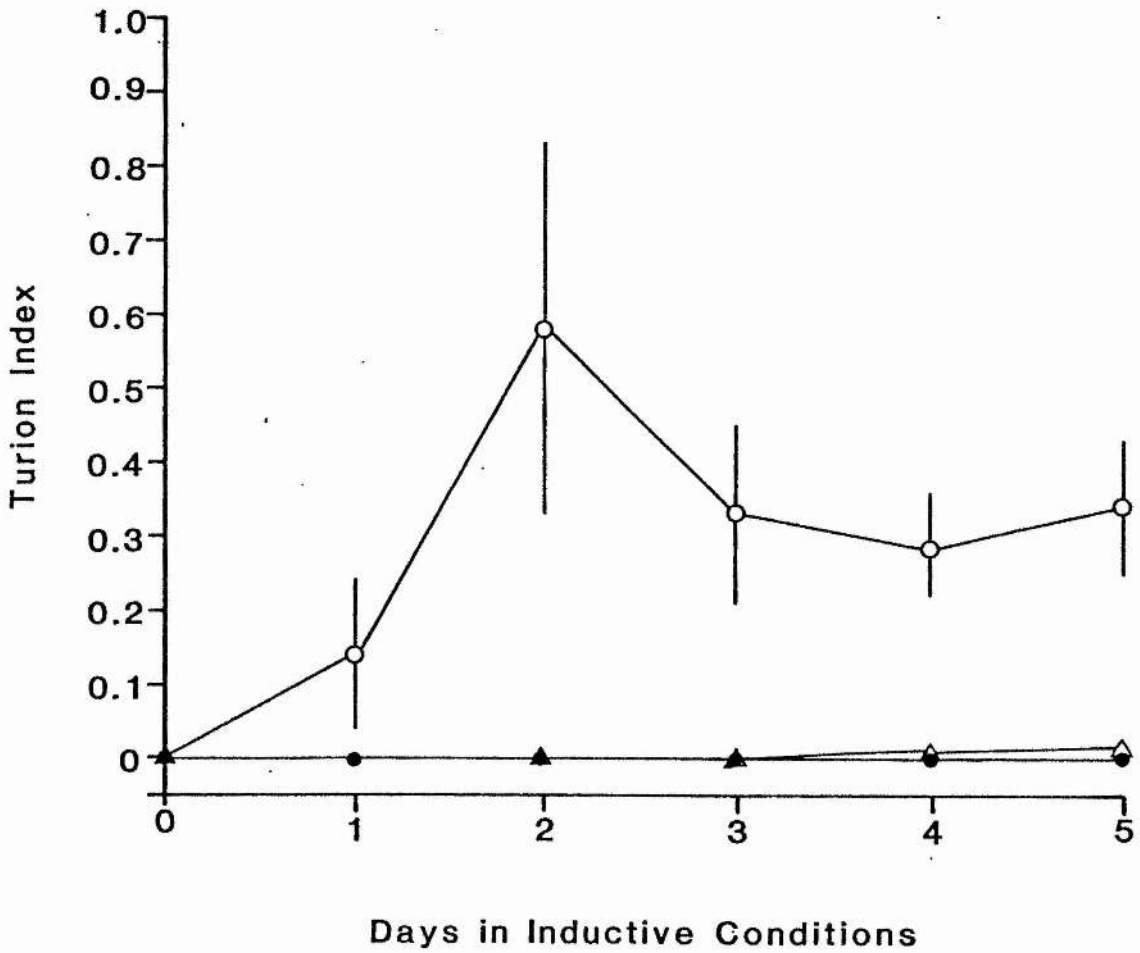
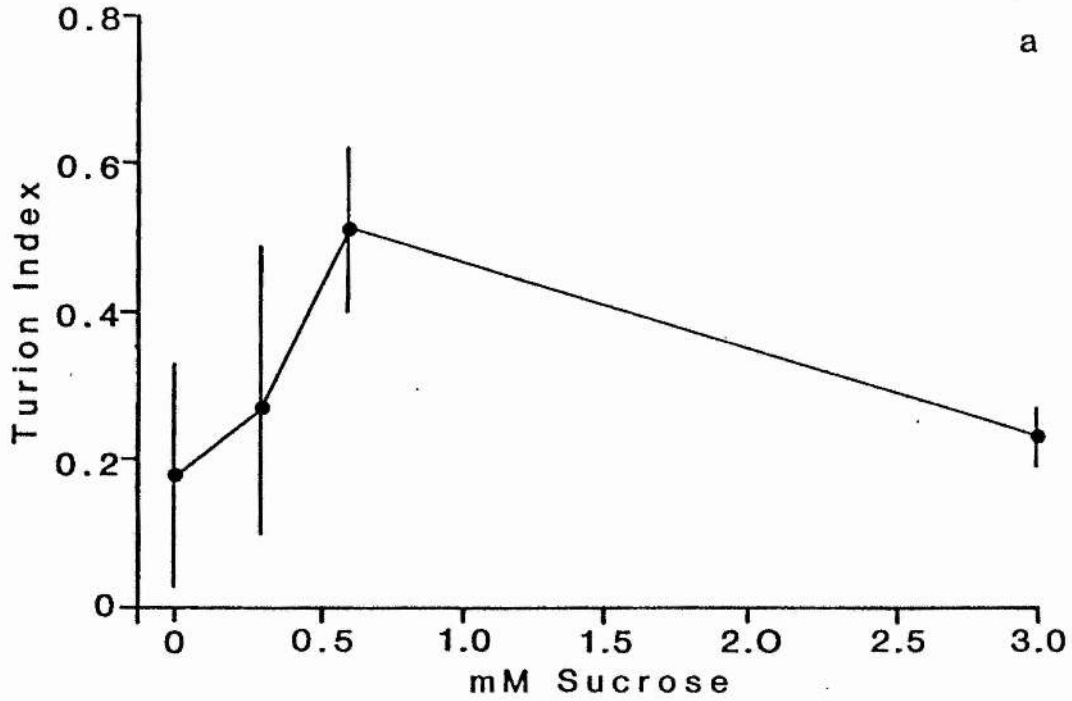

Turion Index
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
1
2
3
4
5
Days in Inductive Conditions

Fig. 7.7. Effect of sucrose concentration on turion production in P. crispus. Plants were grown under short day conditions (10h photoperiod, 400μmole m^{-2} s^{-1} PAR, 30°C temperature, and ζ=12) with an 8h FR end-of-day extension (20μmole m^{-2} s^{-1} PAR).

a. Turion Index

b. Number of days until turions first observed.


a
Turion Index
0.8
0.6
0.4
0.2
0
0
0.5
1.0
1.5
2.0
2.5
3.0
mM Sucrose

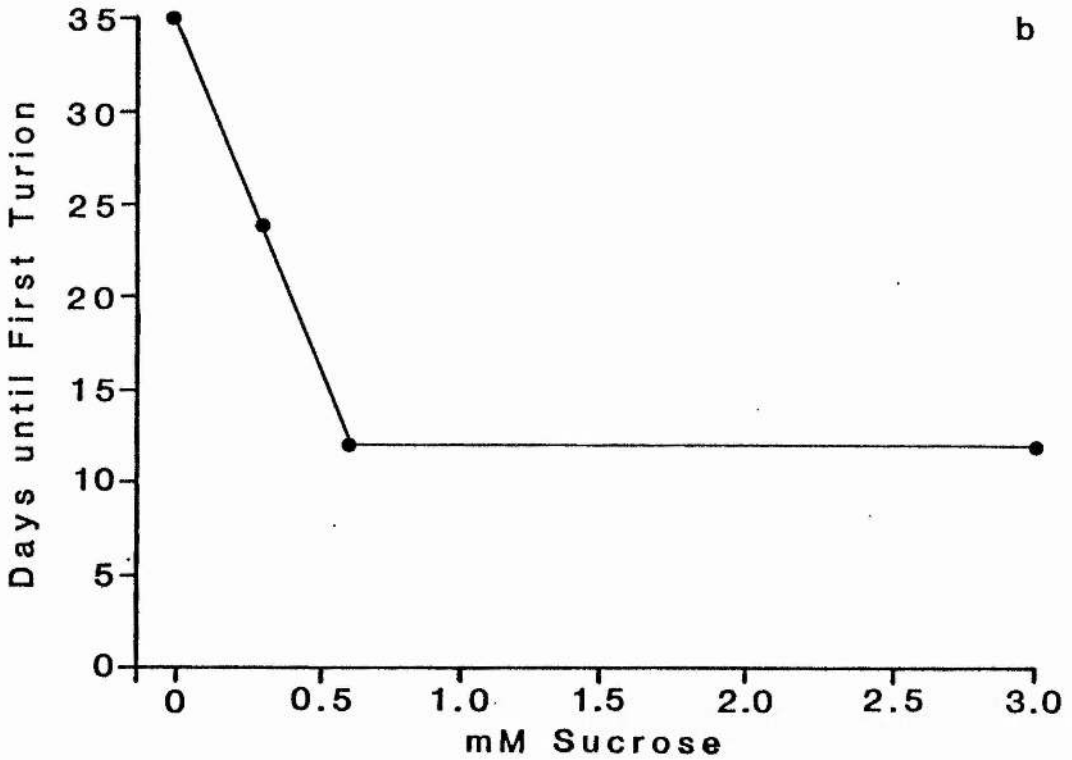

b
Days until First Turion
35
30
25
20
15
10
5
0
0
0.5
1.0
1.5
2.0
2.5
3.0
mM Sucrose

Table 7.1. Turion Index (±S.E.) for P. crispus plants grown at 30°C under varying photoperiodic treatments and sucrose concentrations. During the main photoperiod the PAR photon fluence rate was 400μmole m^{-2} s^{-1} and ζ was 12. (- indicates that the experiment was not conducted.) [a] 80μmole m^{-2} s^{-1}, [b] 25μmole m^{-2} s^{-1}, and [c] 20μmole m^{-2} s^{-1}.

mM Sucrose	10h PAR	10h PAR + 1h R[a] nightbreak	12h PAR	12h PAR + 1h R[b] nightbreak	10h + 8h FR[c] end-of-day extension	10h + 8h R[c] end-of-day extension
0	0	0	0	0.79 ± 0.15	0.18 ± 0.15	-
0.3	0	0	-	-	0.27 ± 0.17	0.19 ± 0.08
0.6	0	-	-	-	0.51 ± 0.11	0.04 ± 0.02
3.0	-	-	-	-	0.23 ± 0.04	-

Table 7.2. Turion Index (±S.E.) and days until First Turion for plants of P. crispus grown in 0.6mM sucrose at 30°C under a 10h photoperiod (400μmole m^{-2} s^{-1} and ζ=12) with an 8h FR end-of-day extension at either 20, 35, or 45μmole m^{-2} s^{-1}.

	FR End-of-Day Extension (μmole m^{-2} s^{-1})		
	20	35	45
Turion Index	0.51 ± 0.11	0.11 ± 0.07	0.13 ± 0.08
Days until first Turion	12	18	18

DISCUSSION

The induction of dormancy in many aquatic angiosperms is controlled by a change in daylength. In cool temperate climates, most aquatic angiosperms enter dormancy in response to short days, often in association with low temperatures (Vegis 1953, Heslop-Harrison 1962, Weber and Nooden 1974, Winston and Gorham 1979). In P. obtusifolius, turion formation is induced by short days in conjunction with high temperatures, however turions are produced by P. crispus in response to long days and high temperatures.

Despite the importance of daylength as a major factor controlling dormancy induction, the action of phytochrome in underwater photoperiodic, as well as photomorphogenetic, responses has rarely been investigated. Furthermore, models of phytochrome action have only considered the photomorphogenetic and photoperiodic responses of green plants in terrestrial systems. Since aquatic angiosperms exhibit phytochrome mediated responses, these models should also be capable of explaining the action of phytochrome in the underwater environment.

In terrestrial systems, it has been proposed that the photomorphogenetic shade responses of green plants are controlled by phytochrome (Cummings 1963, Smith 1975, Morgan and Smith 1976, Vince-Prue 1977, Frankland and Letendre 1978, Child et al. 1981). Plants growing beneath vegetation canopies are subjected to a light environment that differs from daylight in that ζ values are reduced, due to selective absorption of R light by the canopy, and PAR photon

fluence rates are low (Yocum et al. 1964, Holmes and Smith 1977b, Tasker and Smith 1977, Frankland and Letendre 1978, Holmes 1981). In several species, the stem extension response in foliage shade has been found to be primarily controlled by ζ, and hence φ (Morgan and Smith 1976, 1981, Smith and Holmes 1977, Young 1981), whereas specific leaf area was determined by PAR photon fluence rates (Frankland and Letendre 1978, Morgan and Smith 1981). However, in many species, foliage shade responses appear to be controlled by the simultaneous operation of both the static and dynamic modes of phytochrome action (Fitter and Ashmore 1974, Young 1976, Vince-Prue 1977).

The photoperiodic responses of green plants have long been associated with the static mode of phytochrome action (Parker et al. 1946, 1950, Vince-Prue 1975). The amount of phytochrome and its form during and/or at the end of the photoperiod appear to be the most crucial factors in determining photoperiodic responses (King and Vince-Prue 1978, Ohtani and Ishiguri 1979). There is no apparent correlation between prior photomorphogenetic changes and photoperiodic response (Vince-Prue 1977, King and Vince-Prue 1978).

In terrestrial systems, it is proposed that the photomorphogenetic responses of green plants in foliage shade are mediated by both the static and dynamic modes of phytochrome action. In daylight, plants are exposed to high values of ζ and high photon fluence rates; thus, a large φ value and rapid Pfr cycling would be established. However, under foliage shade, low φ values and low cycling rates would prevail. During the day, the two modes of phytochrome action may exhibit an additive, or possibly synergistic,

response to the light climate. The static mode response might also serve to offset perturbations in the cycling rate caused by diurnal fluctuations in the photon fluence rate in response to cloud cover and sun flecks. Photomorphogenetic responses have also shown a Pfr-dependent static mode inhibition which persists for 12 to 16h in darkness (Vince-Prue 1977). Jose and Vince-Prue (1978) proposed that the Pfr established at dusk would not revert to Pr in darkness, but that static mode control by Pfr would continue throughout the night.

Photoperiodic responses operate primarily through the static mode of action in response to the amount of Pfr established at the end of day. However, spectrophotometric measurements have shown that there is a rapid dark loss of Pfr during photoperiodic induction (Vince-Prue et al. 1978). Thus, there may exist pools or states of Pfr with different kinetics of change in darkness (Jose and Vince-Prue 1978). Vince-Prue (1976) proposed that the amount of Pfr present during the night may interact with an endogenous circadian rhythm which exhibits a rhythmic change in sensitivity to Pfr. The lowering of ζ or the cessation of Pfr cycling at dusk may act as the signal for dark timing to commence and serve to synchronize the dark reactions in photoperiodism (Vince-Prue 1976, King et al. 1978, Vince-Prue 1981). The dynamic mode, operating through the day, may also be involved in reactions which are prerequisite for the dark inductive response (Jose and Vince-Prue 1978).

In order to adapt this model of phytochrome action to aquatic angiosperms, the fundamental differences between the light climates of terrestrial and freshwater systems must be considered. In terrestrial systems, natural daylight is characterized by comparatively high ζ values (about 1.3) and high PAR photon fluence rates (about 1800μmole m^{-2} s^{-1}), whereas foliage shade habitats show low ζ values (about 0.2 to 0.4) and low PAR photon fluence rates (Frankland and Letendre 1978). The lake surface is equivalent to an unshaded terrestrial habitat with respect to ζ and PAR values. However, with increasing water depth, the PAR photon fluence rate decreases logarithmically and ζ increases (Figures 4.2 and 4.4). In clear water, high PAR photon fluence rates are always associated with low ζ values and, conversely, low PAR fluence rates always accompany high ζ values, in direct contrast to the terrestrial situation. Furthermore, underwater ζ values exhibit an entirely different range from those of terrestrial systems, with a minimum of 1.2 to 1.4 at the water surface to an infinitely large value at great depth.

The static mode of phytochrome photomorphogenetic action in terrestrial plants under high PAR photon fluence rates is characterized by a hyperbolic relationship between ζ and φ which asymptotes at a ζ value between 2 and 3 (Morgan and Smith 1976, Smith and Holmes 1977, Frankland and Letendre 1978). However, underwater ζ is generally greater than 3 (Figures 4.2 and 4.4), a ratio which, for terrestrial plants, elicits very little change in the photostationary state. In order for the static mode of phytochrome action to operate underwater at high PAR photon fluence rates, aquatic angiosperms must

exhibit a greater sensitivity to changes in large ζ values than has been shown for terrestrial plants. Phytochrome photoequilibria and ζ, and their influence on the photomorphogenetic responses of aquatic angiosperms have yet to be investigated. The relationship between turion production and ζ for P. crispus presents contradictory information, in that the turion index asymptotes at a ζ value of about 2, comparable to terrestrial angiosperms, whereas the response time for turion formation did not asymptote until a ζ value of approximately 8 (Fig. 7.5). If φ is sensitive to changes in large ζ values, then aquatic angiosperms may well employ the static mode of phytochrome action during photomorphogenetic responses in daylight under high PAR photon fluence rates.

However, at low PAR photon fluence rates, the photostationary equilibria may never be attained due to continuous Pfr destruction. Heim and Schafer (pers. comm.), working on etiolated Sinapis alba, report that for R and FR photon fluence rates greater than 2.2μmole m^{-2} s^{-1} and 6.1μmole m^{-2} s^{-1}, respectively, the φ value characteristic of high photon fluence rates was established. In green plants, however, φ may be fluence-rate dependent at slightly higher photon fluence rates as chlorophyll has been shown to decrease the phytochrome signal (Jose et al. 1977, Ohtani and Kumagi 1980). Spence (1981) reported that R and FR photon fluence rates were reduced by approximately 70 and 23 percent, respectively, after passing through a fresh P. crispus leaf. Therefore, R and FR photon fluence rates greater than 4 and 8μmole m^{-2} s^{-1}, respectively, should theoretically establish the maximum φ in P. crispus. Providing that aquatic angiosperms are sensitive to changes in large ζ values, the

static mode of phytochrome action may operate in underwater photomorphogenetic responses during the day. However, if further investigations reveal that aquatic angiosperms display the same ζ sensitivity as terrestrial plants, then the daytime static mode of phytochrome action, which functions only when φ is less than 3, will operate only in aquatic plants situated near the water surface, in dense weed beds, or under persistent algal blooms.

The dynamic mode of phytochrome action, because of its strong irradiance dependency, could operate in aquatic angiosperms as it does in terrestrial plants. At the water surface a rapid cycling rate would be established and this would decline with depth as a function of the PAR photon fluence rate.

Very few investigations have been conducted on phytochrome control of photomorphogenesis in aquatic angiosperms. However, the germination of Spirodela polyrrhiza turions (Czopek 1964) and Potamogeton richardii seeds (Spence et al. 1971b) have been shown to exhibit phytochrome control. The observation that Potamogeton richardsonii, Potamogeton polygonifolius, and P. obtusifolius, when grown under conditions of shade and natural daylight at constant ζ (about 1.2), produced shade leaves with a significantly larger specific leaf area, suggests that the dynamic mode of phytochrome action may control specific leaf area in aquatic, as well as terrestrial, angiosperms (Spence and Chrystal 1970b, Spence and Dale 1978). Phytochrome control has also been implicated in the underwater production of aerial-type leaves in the heterophyllous freshwater macrophyte, Hippuris vulgaris (Bodkin et al. 1980). Laboratory

experiments established that high PAR photon fluence rates (about 1000μmole m^{-2} s^{-1}) and temperatures greater than 10°C were prerequisite for underwater aerial-type leaf production. Under these conditions low ζ, either throughout the photoperiod or as a dim end-of-day extension, produced underwater aerial-type leaves, whereas high ζ, during or after the photoperiod, produced submerged leaves. Thus, the static mode of phytochrome action appears to be controlling leaf morphogenesis. Under natural conditions, the ζ values at the depths of transition from submerged to aerial-type leaf production were 5.83 and 13.2 for the two lakes studied. If this response was controlled by the static mode of phytochrome action, and hence φ, then these plants lend credence to the hypothesis that aquatic angiosperms are more sensitive than terrestrial plants to changes in large ζ values. However, the observation that underwater aerial-type leaves were not produced under low PAR fluence rates (200μmole m^{-2} s^{-1}) and low ζ, although the plants were rich in carbohydrate (Bodkin 1979), suggests that an underlying dynamic mode of phytochrome action may also regulate heterophylly in H. vulgaris.

Photoperiodic responses, because they operate through the static mode of action in response to the amount of Pfr established at the end of day, could operate in aquatic angiosperms as they do in terrestrial plants. In the underwater environment, twilight is characterized by a decrease in ζ, proportional to or greater than that observed in terrestrial systems (Figures 5.1, 5.2, and 5.3). These large ζ shifts in conjunction with very low photon fluence rates may act as the signal for dark timing to commence, as was postulated for terrestrial plants. Many photoperiodic phenomena have been reported

for aquatic angiosperms, including flowering in Lemna gibba and Lemna minor (Krajncic and Devide 1980), turion germination in Myriophyllum verticillatum (Weber and Nooden 1976a), and turion production in Pinguicula grandiflora (Heslop-Harrison 1962), Myriophyllum verticillatum (Weber and Nooden 1974), Utricularia vulgaris (Winston and Gorham 1979), and in P. crispus and P. obtusifolius, as reported here. However, with the exception of this investigation on turion production in P. crispus, phytochrome control has not been directly implicated in the induction of dormancy in aquatic angiosperms.

The high temperature requirement for dormancy induction in both P. crispus and P. obtusifolius appears incongruous with respect to their cosmopolitan distribution, in particular the former species which is often regarded as a weed (Ogden 1943, Nasar and Munshi 1978, Nicholson 1981). P. crispus is native to southern Europe, however it now extends throughout Europe, Asia, Africa, Australia, and North America (Fryer et al. 1915, Hagström 1916, Tutin et al. 1980), with a northern limit of about 60°N (Hagström 1916). In Long Loch and Loch Drumore, both 56°N, P. crispus is approaching the northern extent of its range. The very limited turion production by P. crispus populations in these lakes concurs with the experimental data presented here, which show that the critical temperature for turion formation under long day conditions (18h) is about 16°C. Summer temperatures in Long Loch and Loch Drumore were between 17°C and 20°C (Figures 4.10 and 4.11), and consequently turion production was minimal. At more equatorial latitudes, turion production by P. crispus is reportedly much greater. Near Chiba, Japan (35°38'N) P. crispus produced about 800 turions per square meter (Sastroutomo et

al. 1979, Sastroutomo 1980), whereas turion density was 1320±170 m^{-2} in a South African lake (27°30'S) (Rogers and Breen 1980). During the period of visible turion development the average daylength was 14.5h and 12h, respectively, and the water temperature in both lakes was between 18 and 25°C.

P. obtusifolius, a native of northern Europe, has extended south over most of Europe and across to Asia, Greenland, Canada, and the northern United States (Fryer et al. 1915, Tutin et al. 1980). Unlike some temperate climate aquatic species, turions are produced in response to short days in association with high temperatures, conditions characteristic of late summer and early autumn. Although initiated early in the growing season, the turions are not released until early winter and thus serve the same function as those of most aquatic angiosperms, namely perennation. The early onset of dormancy in this species may represent an adaptation to its native distribution and deep water habitat (Spence and Chrystal 1970a). In north temperate climates, the rapid decline in air temperature during autumn causes only a gradual decrease in water temperature which, depending upon basin morphometry and prevailing meterological conditions, may not penetrate the lower limits of macrophyte colonization until late autumn. At that time, the PAR photon fluence rate, particularly at depth, may not be permissive for carbohydrate storage and turion development. P. obtusifolius appears to circumvent this potential problem by initiating turion formation at the end of summer when both temperatures and PAR photon fluence rates are still conducive to carbohydrate accumulation. The long period of maturation of the turion on the parent plant and its release in late autumn through

decomposition of the parent plant ensures that conditions are unfavourable for turion germination until the following spring.

In P. crispus, however, the rhizome system persists throughout the year. The turions, which are produced midsummer, germinate in the autumn and each may yield as many as seven independent shoots or rhizome systems. Thus, the turions of P. crispus are not strictly perennating organs, but function primarily as propagules. This strategy, encompassing maximal vegetative production during the winter months, a persistent rhizome system, and turions which function primarily as propagules, permits colonization of areas otherwise occupied in the summer by annual species and may have contributed to the success of this species when introduced to the lakes of central North America.

SUMMARY

In P. obtusifolius, turion formation is induced by short days in conjunction with high temperatures, whereas turions are produced by P. crispus in response to long days and high temperatures. The long days represent a photoperiodic signal which has been shown for P. crispus to operate through the static mode of phytochrome action.

Phytochrome-mediated photoperiodic responses are characteristically dependent upon the amount of Pfr established at the end of day. In terrestrial systems, the twilight shift in the ratio of the R to FR wavelength bands, in conjunction with a reduction in the PAR photon fluence rate, may function as a photoperiodic clock and determine the end-of-day φ. In the underwater environment, twilight is characterized by a reduction in ζ, proportional to or greater than that observed in terrestrial systems. Thus, the photoperiodic responses of aquatic angiosperms could exhibit the same control mechanism as those of terrestrial plants, in that daylength is perceived by changes in both light quality and quantity, and the magnitude of the photoperiodic response is determined by the end-of-day φ.

Under laboratory conditions, where light quality remains constant throughout the photoperiod, the change in the PAR photon fluence rate may act as a regulator of photoperiodic timing. The end-of-day value of ζ, and hence φ, is equivalent to that present throughout the photoperiod. Thus, the magnitude of the photoperiodic response would be controlled by both the duration and the ζ value of the

experimental photoperiod. In P. crispus, laboratory experiments established that both the magnitude and rate of turion production under inductive conditions of long days and high temperatures were controlled by the value of ζ during the photoperiod.

Thus, turion production in P. crispus was found to be controlled, qualitatively, by temperature and photoperiod and, quantitatively, by the photoperiodic ζ value, which determines φ, and PAR photon fluence rate, which determines the photosynthate concentration.

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